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FORM, FUNCTION AND PATHOLOGY IN THE PANTROPICAL SPOTTED DOLPHIN (*STENELLA ATTENUATA*)

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Stenella attenuata
(photograph by Robert Pitman, Southwest Fisheries Science Center, La Jolla, CA)

INTRODUCTION

The pantropical spotted dolphin (*Stenella attenuata)* is found worldwide, primarily in tropical waters (Perrin et al. 1987, Perrin 2009) but has received the most attention in the eastern tropical Pacific Ocean (ETP) where mortality due to the yellowfin tuna purse-seine fishery between about 1960 and 1980 reduced one population to depleted status (Smith 1983), leading to decades of research directed toward population recovery. Subsequent to 1990, changes in fishery operations dramatically decreased fishery-related mortality, but spotted dolphin abundance has not recovered as expected (Wade et al. 2007). In an effort to determine whether factors related to form, function and or pathology in spotted dolphins may be contributing to this apparent lack of population recovery in the ETP, we reviewed spotted dolphin literature available through 2012. We relate the results of this literature review to potential interactions with the ETP tuna purse-seine fishery. Although the majority of the data were collected from specimens killed in tuna purse-seine nets in the ETP, we reviewed and include results of studies without regard to geographic origin.

This review is restricted to the pantropical spotted dolphin (including subspecies and or management stocks such as the coastal spotted dolphin *Stenella attentuata graffmani*) and generally includes comparative information on other cetacean species only when such information was included in a reviewed spotted dolphin article. Thus the review includes very little information regarding other species of closely-related small delphinids (e.g., the Atlantic spotted dolphin, *Stenella frontalis,* the spinner dolphin *Stenella longirostris,* or the striped dolphin *Stenella coeruleoalba*). Going forward in this review, we refer to the pantropical spotted dolphin (*Stenella attenuata*) as simply "spotted dolphin".   We discuss the major organ systems in alphabetical order, for ease of reference. The depth and breadth of various sections vary considerably, based on the amount of information available. In many sections, information from the original references is taken verbatim or roughly paraphrased.   Where successive sentences are drawn from a single reference, the source is indicated after the first and last sentence in the series. Where all information in a single paragraph is drawn from a single source, the source is indicated following the first and last sentence in the paragraph.

Initial sections of this review focus on form of various organ systems and discuss functional aspects where known. Subsequent sections are devoted to External Characteristics, Hydrodynamics, Thermodynamics (heat flux), Development (prenatal, perinatal, and postnatal periods), and Distress, Disease and Death. The penultimate section summarizes Implications for Fishery Effects, emphasizing morphological and/or physiological characteristics of spotted dolphins that may contribute to lack of ETP spotted dolphin population recovery. We conclude with a summary.

ACOUSTIC SYSTEM

Cetaceans, including spotted dolphins, communicate primarily via acoustic rather than visual means because sound transmission is more reliable and efficient in aquatic habitats given the speed with which sound travels through water and the uninterrupted availability of sound transmission throughout both day and night. This dependence on

sound has led to extensive inter-related modifications of sound reception and production anatomy, including:

(1) "telescoping" of the skull such that the jaw bones have slid over other skull bones, the nostrils have moved from the front of the face to the top of the head (Norris 1968, Wartzok and Ketten 1999), and the forehead has become dish-shaped to contain a melon and nasal sacs which function in sound production and focusing (Ketten 1992b);

(2) reduction or elimination of external auditory canals (Reysenback de Haan 1966, Ketten 2000, Nummela 2009);

(3) development of alternative routes for sound reception via specific lipid composition and topographies in the lower jaw bone (Litchfield et al. 1975, Varanasi et al. 1975, Koopman et al. 2006);

(4) acoustic isolation of each ear from bone conduction via the skull, accomplished by encasing each middle and inner ear in a foam-filed parasinus (the tympano-periotic complex, TPC) located outside the skull and suspended by ligments rather than bony connections (Reysenback de Haan 1966, Wartzok and Ketten 1999, Nummela 2009);

(5) development of massive middle ear bones connected stiffly together by a firm bony ridge, ligments, and a membraneous sheath, in contrast to the highly moveable ossicular joints found in terrestrial mammal ears (Wartzok and Ketten 1999, Ketten 2000);

(6) adaptation of the inner ear to facilitate extremely supersonic hearing, with a relatively large cochlea and reduced vestibular apparatus (Reysenback de Haan 1966, Ketten 2000)

(7) development of a system of air-filled nasal sacs for producing whistle and echolocation click train sounds (Evans and Prescott 1962, Cranford et al. 1996); and

(8) development of specific lipid compostitions and topographies within the melon that function to focus the outbound echolocation clicks (Varanasi and Malins 1971, Cranford et al. 1996).

Sound Reception. Modifications (1) - (6) facilitate sound reception, transforming incoming mechanical energy within the range of about 5 kHz to 100 kHz (Ridgway 2000) into nerve stimulation enroute to the brain. Sound enters the head via a complex lipid structure encased by the lower jaw (Mohl et al. 1999, Koopman et al. 2006). These lipids are composed of endogenously synthesized acoustic fats theoretically functioning to slow and focus incoming sound waves to the ear area at the caudal end of the lower jaw (Koopman et al. 2006). Spotted dolphin jaw fat is dominated by iso 5:0FA (10-48%) and iso 15:0FA (5-31%), but also includes high concentrations of 16:0ALC (20-60%) wax-ester alcohol and iso15:0ALC (7-24 %) (Koopman et al. 2003).

Incoming sounds pass from these jaw lipids into the adjacent TPC, which has adapted to accommodate the increased sound speed, impedance mismatch, and increased pressure associated with aquatic surroundings (Ketten 1992a). The TPC includes two connected capsules (bullae), the *tympanic* bulla enclosing the middle ear structures and the *periotic* bulla enclosing the inner ear structures (Ketten 1992a).   The right TPC is

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located slightly anterior to the left TPC (Ketten and Wartzok 1990) near the left and right bases of the lower jaw, with the tympanic plate of the tympanic bulla facing toward a thinned area of jaw bone (the pan bone) (Ketten 1992b) on each side of the head (Hemila et al. 1999). Tympanic bulla morphology varies between species within the Delphinidae (Kasuya 1973), being much smaller in spotted dolphins than bottlenose dolphins, but the functional significance of this difference is unknown. Incoming sound enters the tympanic bulla by crossing the bony tympanic plate, then progresses through a highly modified series of middle ear bones and into the cochlear structures of the inner ear (Ketten 2000) where cochlear hair cells convert the incoming mechanical acoustic energy into nerve impulses which travel to the brain via an an enlarged eighth nerve (Ridgway 2000). The middle ear is adapted for acoustic isolation and for withstanding pressure changes while the inner ear is adapted for ultrasonic perception (Ketten 1992a).

The middle ear is isolated acoustically by ligamentous rather than bony connections to the adjacent skull, so that sound arrives separately at each inner ear only via the middle ear bones (Ketten 1992a). Directional hearing in spotted dolphins may be facilitated by this acoustic isolation of the left versus right ears, combined with the slight asymmetry in TPC placement on either side of the head. The tympanic bullae of the middle ear contain the same three ear bones (ossicles; malleus, incus and stapes) as terrestrial mammals, but these structures are rigidly-joined and very dense, presumably to resist compression during large pressure changes while swimming and diving (Ketten 1992b, Cuspinera-Mercadillo et al. 1994) to facilitate the broad-band ultrasound transmissions associated with echolocation clicks (Ketten 1992a). These departures from the typical middle ear formation of terrestrial mammals facilitate sound reception underwater, as opposed to hearing in air. Whereas the ossicles in the ears of terrestrial mammals transmit vibrations from the tympanic *membrane*, reduce the velocity, and amplify *pressure* at the oval window, the ossicles in cetacean ears transmit vibrations from the tympanic *plate* to the oval window and there amplify the *velocity* rather than the pressure.

The spotted dolphin inner ear is also highly modified compared to terrestrial mammals, and differs even from that of mysticetes, particularly with respect to the basilar membrane and the spiral laminae, reflecting the importance of ultrasonic echolocation signal processing for odontocetes (Wartzok and Ketten 1999). Modifications include large increases in the number of acoustic processing cells, ganglion cell:inner hair cell ratio, and basilar membrane thickness to width ratio (Ketten 1992a). Spotted dolphin ear dimensions are similar to those in other closely-related odontocetes (e.g., *Delphinus delphis, Tursiops truncatus*), with a basilar membrane length of about 37 mm, auditory ganglion cell abundance of about 82,000 cells, average cochlear cell density of about 2200 cells/mm (compared to human ganglion cell density of about 984 cells/m) and ganglion cell:hair cell ratio of about 4.4:1 (compared to about 2.4:1 in humans) (Wartzok and Ketten 1999).

Spotted dolphin inner ear morphology is typical of Type II odontocetes, based on the structure of the inner and outer ossified spiral laminae (Ketten 1992a). Type I and

Type II odontocetes are distinguished by differences in frequency processing and habitat. Type I odontocetes process higher frequencies (> 100 kHz) than Type II odontocetes (40-80 kHz), and tend to occupy inshore, turbid habitats where these higher frequencies are more effective for determining fine details of nearby objects. Type II odontocetes tend to occupy offshore and pelagic habitats with higher water clarity and fewer objects, where relatively long-range detection is important (Ketten and Wartzok 1990, Ketten 1997). Spotted dolphin Type II cochlear morphology includes 2.5 turns forming equiangular spirals, 8.4mm outer lamina, 20/40 um base thickness/width ratio, 5/400 um apex thickness/width ration, 0.509 basal ratio and 0.013 apical ratio (Ketten 1997) and a nearly square basilar membrane cross-section that thins and broadens apically (Ketten 1992a).

Sound Production. Modifications (7) and (8) (air-filled nasal sacs and complex lipid topography in the melon) facilate sound *production* by spotted dolphins. Sounds are produced by air movements between various internal sinuses in the nasal area, without moving air into or out of the dolphin's body (Norris 1968, Cranford 2000, Tyack 2000). The sound-producing nasal tissue complex in spotted dolphins is similar to that found in at least 18 other species of odontocetes (Mead 1975, Arvy 1977a, Cranford et al. 1996). This tissue complex includes a frontal concavity occupied by up to five (usually four) (Mead 1975) asymmeterically distributed nasal sacs or divericulae and the melon, a unique elliptical multi-layered mass of fibrous tissue and fats. The nasal anatomy of the spotted dolphin is especially similar to that of the bottlenose dolphin, *Tursiops truncatus* and the common dolphin, *Dephinus delphis* (Mead 1975). The nasal diverticulae act as pressure-driven sound generators that produce clicks when the "pneumatic" lock of the ridged nasal flaps is forced open by sudden expulsion of air from the sacs (Cranford et al. 1996). Specific structures include a small pair of fatty bursae embedded in a pair of connective tissue lips, a cartilaginous blade, a stout ligament, and an array of soft tissue air sacs (the monkey lips/dorsal bursa complex, MLDB) (Cranford et al. 1996). Sounds produced by the MLDB complex in spotted dolphins are likely transmitted to the environment in a manner similar to that in other odontocetes, whereby a complex lipid topography in the melon functions as a focusing transmission organ for outgoing ultrasonic echolocation signals and burst pulse clicks (Varanasi et al. 1975, Ketten 1992a, Koopman et al. 2003). As in other odontocetes, the facial asymmetry of spotted dolphins (including asymmetry in the air sacs) (Mead 1975, Houser et al. 2004) probably contributes to the great variety of sounds produced by these animals (Cranford et al. 1996).

Spotted dolphins use these modified acoustic structures to produce two basic types of sound in both captive and free-ranging conditions: 1) whistles, which tend to be narrow-band relatively low-frequency sounds and 2) ultrasonic click trains, which include both broad-band pulsed sounds and echolocation clicks (Evans 1967, Caldwell et al. 1970, Wartzok and Ketten 1999, Lammers et al. 2006). Whistles tend to be longer-duration, frequency-modulated (FM) signals apparently used for communication between two or more animals emitting and receiving sounds as an interacting group (Smolker et al. 1993, Norris et al. 1994, Lammers et al. 2006). Pulsed ultrasonic click trains apparently are also used for communication and have extremely short-duration interclick

intervals (0.5-1.0 ms) (Au 1993). Echolocation ultrasonic click trains are used for locating prey or examining other nearby solid objects, and generally have peak energy between 20 and 200 kHz (Ketten 1992b), with interclick intervals of 15-45 ms (Au 1993).

Maximum acoustic energy of spotted dolphin whistles tends to occur in the range 3-25 kHz (Hohn and Benson 1990, Moore 1990, Wang-Ding et al. 1995, Oswald et al. 2007), although whistles can reach as high as 150 kHz (Evans 1967, Diercks 1972), as in other long-beaked delphinids including common, bottlenose, striped and spinner dolphins (Oswald et al. 2003). Specific spotted dolphin whistle characteristics vary somewhat between different studies, within the ranges mentioned above. Evans (1967) found that spotted dolphin whistles started at 8-10 kHz or 12-13 kHz and increased to 24-28 kHz, during 0.6-0.8 s as the dolphin simultaneously produced 8-15 very intense clicks per second. Other studies found that spotted dolphin whistle frequencies ranged from 3-21 kHz, with most of the signal in the range 7-18 kHz (Wang-Ding et al. 1995, Wartzok and Ketten 1999). In the eastern tropical Pacific Ocean (ETP), whistles of free-ranging spotted dolphins peak at about 25 kHz, with average beginning and ending frequencies of about 10 and 15 kHz, average minimum and maximum frequencies of about 8.5 and 18 kHz, average duration of about 0.75-0.9 s, and an average of about 1.3-1.9 inflection points and 3 steps per whistle (Hohn and Benson 1990, Moore 1990, Oswald et al. 2007). Whistles recorded from coastal spotted dolphins (*S. attenuata graffmani*) in the ETP are very similar to those of the offshore form (*S.attenuata attenuata*), exhibiting a variety of whistles that sweep up or down and often contain level portions, with looped whistles occuring rarely (Moore 1990). ETP spotted dolphins also produce rapid-succession sounds (chirps), predominantly in the frequency range 6-16 kHz (Moore 1990).

Echolocation signals of free-ranging spotted dolphins are similar to those of other delphinids, typically consisting of broadband, short duration click signals (<80 µs) with a bimodal spectrum: a low-frequency peak occurring between 30-50 kHz, and a high-frequency peak between 80-120 kHz (Au and Benoit-Bird 2003). Echolocating spotted dolphins employ a different strategy than their terrestrial analog, echolocating bats, by varying transmission characteristics of their echolocation system rather than receiver characteristics. Spotted dolphins decrease the transmission level of their echolocation signal as they approach a school of prey (i.e., a collection of many sound scatterers creating volume reverberation) thereby generating nearly constant amplitude during the approach (Au and Benoit-Bird 2003).

CARDIOVASCULAR SYSTEM
No studies specifically address morphology of the cardiovascular system in spotted dolphins but some information exists regarding blood chemistry of various tissues and organs, primarily addressing adaptations related to prolonged breath-hold during diving. In general, spotted dolphins appear to conform to the concept that marine mammals do not possess unique enzyme mechanisms for anaerobic metabolism while diving, and under normal conditions they probably do not often dive long enough to induce anaerobic metabolism. However, spotted dolphins appear capable of the typical marine mammal dive response (cardiovascular adjustments coupled with specific tissue

and organ adaptations) in reaction to unusually long dives. Tissue adaptations include high oxygen carrying capacity and high buffering capacity in both blood and muscle (Castellini 1981).   High oxygen carrying capacity extends aerobic time limits for dives, and high buffering capacity prevents adverse changes in pH despite lactic acid buildup, particulary after a dive when muscle circulation resumes and lactic acid floods into the bloodstream (Castellini 1981).

Concentrations of serum or plasma glucose, urea and blood urea nitrogen, and potassium (Malvin and Rayner 1968) are consistent with results from other Cetacea (De Monte and Pilleri 1984). As in other delphinids, including *T. truncatus* and *L. obliquidens* (Castellini et al. 1992), the ratio of red blood cells to plasma in spotted dolphins is similar to or higher than the ratio found in primates and humans (about 1.2 vs. about 0.9), and is much higher than that found in most other mammals (about 0.4). This high ratio creates high levels of total glucose in the blood and likely facilitates glucose transfer to the central nervous system, in order to support the high glucose metabolism associated with the large odontocete brain (Castellini et al. 1992).   Dolphin blood is similar to human blood in supporting rapid transport of glucose in and out of the red blood cells, facilitating rapid delivery of glucose to central nervous system (CNS) tissues including the brain.   This is particularly important because the CNS has no internal glycogen stores. When the CNS demand for glucose increases during low-oxygen conditions such as diving for long periods, high total glucose concentration in the blood and rapid transport rates become especially important (Castellini et al. 1992).

Measurements of metabolic enzyme activities, muscle myoglobin content, and muscle buffering capacity in various body components (muscle, heart, brain, kidney, liver, lung, and diaphragm) of 4 adult spotted dolphins killed during tuna purse-seine operations in the eastern tropical Pacific Ocean indicate that these dolphins are generally similar physiologically to other marine mammals studied in terms of adaptations to living in the ocean environment (Castellini 1981). Oxidative enzymes (lactate dehydrogenase (LDH), pyruvake kinase (PK), and citrate synthase (CS)) and their characteristics are generally similar to those of terrestrial mammals, while muscle myoglobin content and buffering capacity are much higher, reflecting the diving requirements of mammals foraging in an aquatic environment (Castellini 1981).

Activity of LDH (U gm^{-1}; 37 ^{o}C) in abdominal and swimming muscles of spotted dolphins averaged 1016 ± 375 for the pyruvate to lactate direction, and 283 ± 102 for the lactate to pyruvate direction (Castellini 1981). Both measures are in the mid- to high range of activities in the marine and terrestrial species sampled. In body compartments other than muscle (i.e., heart, lung, brain, liver, kidney and diaphragm), LDH activity (pyruvate to lactate) of spotted dolphins is low to mid-range compared to other marine mammals.   Reverse LDH activity (lactate to pyruvate) varied from very low to moderately high in the same organs, being significantly higher than concentrations found in kidneys from terrestrial species (Castellini 1981).

Activity of PK in spotted dolphin skeletal muscle averaged 1099 ± 280 (U gm^{-1}, 37 $^{\circ}$C) (Castellini 1981). This value is similar to that found for rabbit muscle, but much higher than that measured in other marine (about 500-800) and terrestrial (about 400 to about 700) mammals. The high levels in muscle of both spotted dolphins and rabbit may be related to sprinting abilities. Buffering capacity of swimming muscle was also higher in spotted dolphins (87-84 µmoles NaOH gm tissue^{-1}; pH unit [6-7]) than in other marine mammal species tested (72.1 $\pm$ 0.9), and tended to be similar to that in the rabbit, again perhaps related to a capacity for short-term burst activity using muscle with high glycolytic potential (Castellini 1981). Activity of PK in spotted dolphins organs was generally lower than in organs of most other species examined (Castellini 1981), perhaps reflecting a relatively reduced ability to withstand hypoxia.

Activity of CS in spotted dolphin muscle (21 U gm^{-1}; 37 $^{\circ}$C) was about average compared to other species tested, while CS activity in organs tended to be in the mid to high ranges compared to other species (Castellini 1981). Activity in the heart was 74 $\pm$ 4.6, toward the high end of the range for all mammals tested, while CS activities in liver (4.8) was about average compared to the other species tested. Muscle myoglobin concentration in spotted dolphins is much higher than in terrestrial mammals, reflecting an ability to carry more tissue oxygen, but is in the low to mid-range compared to other marine mammals (2.54 $\pm$ - 0.75 gm Mb/100 gm tissue) (Castellini 1981), perhaps reflecting their relatively short-period diving habits (Scott and Chivers 2009) relative to some other species.

DIGESTIVE SYSTEM

Morphology. The spotted dolphin digestive tract is morphologically similar to that of other small delphinids (Harrison et al. 1966). The stomach consists of four chambers: the forestomach, main stomach, connection chamber, and pyloric stomach (Mead 2009). Food is ingested whole and passes unchewed through the pharyngeal food channel and into the forestomach. The oesophagus lacks glands. The dilatable, muscular forestomach is lined with a thick, stratified squamous epithelium. Many cells of the stratum spinosum contain fat globules. The forestomach leads by a narrow opening into the glandular main stomach, which has a thick spongy mucosa containing extensive pits and glands. Mucus, symogen and parietal cells are present; the latter appear more common than in other mammals. Digestion begins primarily in the main stomach, although some digestive fluids may enter the forestomach and initiate some pre-digestion. From the glandular main stomach an even narrower opening leads to a small curved and subdivided connecting channel which opens by a valvular slit into the tubular pyloric stomach, which is lined with mucus-secreting cells. This chamber lacks folds and terminates at a sphincter leading into a dilated proximal duodenum. From the duodenum, digesta enter the intestinal area, where digestion continues and absorbtion commences.
 The elongated intestine is large proximally, with villi. The crypts of Lieberkuhn contain many goblet cells and mitotic figures. Paneth and argentaffin cells are absent. There is no caecum or clear demarcation between small and large intestine, where digestion continues and absorbtion begins. Villi are absent in the lower intestine where

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considerable accumulations of lymphoid tissue lie in the lamina propria (Harrison et al. 1966).

The mean intestine length of adult spotted dolphins (189-191 cm) is about 1670 cm, and the mean ratio of intestine length to body length is about 8.8 (Nakajima et al. 1967). This ratio is similar to that in several other dolphin species (e.g., *Stenella coeruleoalba*, *Delphinus delphis, Grampus griseus, Lagenorhynchus obliquidens,* and *Feresa attenuata),* but is noticeably lower than in *Tursiops truncatus* (mean ratio about 13.0) and higher than in *Steno bredanensis* (mean ratio about 4.9) (Nakajima et al. 1967). These differences may relate to differences in food habits, although no studies have been conducted to investigate this possibility.

Although not reported for spotted dolphins, the closely-related *Stenella coeruleoaba*, as well as other delphinds (e.g., *Delphinus delphis, Phocoena phocoena,* and *Didelphis* capensis) has an Aselli's Pseudopancreas (AP, or *Nodi lyphatici mesenterici*), a digestive structure similar to that found in the dog but not in man (Pilleri and Arvy 1971). The AP projects from the mesentery, in which it is embedded, near the pancreas and is a very large assemblage of lymphatic tissue. The AP appears to be the first important relay for the molecules that pass through the intestinal wall during digestion, facilitating slow circulation of chyle and prolonged contact with the lympoblasts and immunoblasts of the lymphatic tissues. Its large size implies it is more important than the spleen (Pilleri and Arvy 1971).

As in terrestrial mammals, the spotted dolphin liver contains specialized macrophage Kupffer cells (Kawashima et al. 2004b). These cells are located on "top" of the hepatocytes and project into the blood stream of the kidney. Their function is removal of particulate contaminants, endotoxins, aged erythrocytes, and other noxious substances from circulation. Kupffer cell abundance in various hepatic lobular zones of spotted dolphins is reversed from the pattern seen in terrestrial mammals, being greatest in the peri-venous zone, intermediate in the mid-zonal region, and least common in the peri-portal region.   Although the spotted dolphin was the smallest of five cetacean species examined, it had the greatest frequency of Kupffer cells (Kawashima et al. 2004b). The Kupffer cells contained black and yellow liposfusin-based pigments, but the functional significance of these findings is unknown (Kawashima et al. 2004b).

Diet. Spotted dolphins appear to feed primarily at night, based on the observation that fresh prey is most often found in stomachs in early morning (Scott and Cattanach 1998). Food tends to include both epipelagic and mesopelagic prey (Shomura and Hida 1965, Fitch and Brownell 1968, Perrin et al. 1973, Bernard and Hohn 1989, Robertson and Chivers 1997), with larger dolphins eating larger prey items (Robertson and Chivers 1997). Prey composition in forestomachs varies seasonally and geographically, and includes at least 56 species of fish and 36 species of cephalopods, primarily mesopelagic species (Robertson and Chivers 1997). Lactating females tend to have fuller stomachs than non-lactating females (16%-24% more full) and may sometimes prefer

ommastrephid squid to fish prey (Bernard and Hohn 1989), although fish is generally preferred over squid (Robertson and Chivers 1997).

The diet of spotted dolphins can be expected to include a relatively high concentration of n-3 fatty acids, because the marine food chain is based on n-3-rich plant life. Likely reflecting this food composition, the adipose tissues of spotted dolphins tends to contain more n-3 fatty acids than typically terrestrial-based n-6 fatty acids (Williams et al. 1987). However, membrane lipids of more metabolically active tissues (liver and muscle) in spotted dolphins tend to contain more n-6 fatty acids than n-3 acids (Williams et al. 1987). This pattern of higher n-3 concentration in adipose tissues and higher n-6 concentrations in more active tissues is similar to that seen in terrestrial mammals (e.g., zebra, giraffe), and may reflect the evolutionary background of spotted dolphins, as marine mammals descended from formerly terrestrial mammals, specifically the artiodactyls (Price et al. 2005). Sources of n-6 fatty acids in spotted dolphins may include both diet and preferential deposition.

ENDOCRINE SYSTEM

Research on the endocrine system in spotted dolphins has focused on the adrenal gland and its role in the alarm response. The adrenal gland in spotted dolphins (and the closely-related *Stenella longirostris*) is approximately triangular in cross-section, and as in other mammals including other cetaceans, includes an outer zoned cortex surrounding a central medulla (Clark et al. 2008). Adrenal gland percent cross-sectional area (PCA) in spotted dolphins is approximately 64.4% cortex, 29.4% medulla, and 6.2% "other", irrespective of gender or sexual maturity. In spotted dolphins the adrenal gland is surrounded by a connective tissue capsule which projects deeply into the cortex creating a lumpy appearance of varying degree. As in other mammals, the spotted dolphin adrenal cortex includes three zones; the zona glomerulosa, zona fasciculata, and zona reticularis. The spotted dolphin medulla projects into the cortex, similar to the medulla of the bottlenose dolphin (*Tursiops truncatus*). Cortex to medulla ratio in spotted dolphins averaged 2.34 (s.d. 0.79) (compared to 2.46 (s.d. 0.18) in female *Stenella longirostris* and 3.21 (s.d. 0.24) in male *Stenella longirostris*) and did not differ with gender or sexual maturity. This ratio reflects the relatively large cortex and smaller medulla in spotted dolphins and is higher than in *Tursiops truncatus* but within observed variability among cetaceans. The larger cortices observed in spotted dolphins may indicate an especially sensitive "flight or fight" response (i.e. predator avoidance) mediated by cortical hormones. Both spotted dolphins and *Stenella longirostris* appear to restrict adrenaline-producing cells in the adrenal to a distinct band along the outer medulla, a characteristic shared with *Tursiops truncatus* as well as the evolutionarily-related ungulates (Clark et al. 2008).

INTEGUMENTARY SYSTEM

Spotted dolphin skin appears to act as a typical vertebrate integumental defense system, although as in other cetaceans, spotted dolphin skin lacks skin glands, having instead an "even, gel-coated surface of the *stratum corneum,* the cells of which display unfavorable conditions for the attachment of biofoulers such as biofilm-forming diatom,

fungi, and bacteria" (Meyer and Seegers 2004). This thick integument produces the antibiotic compounds lysozyme and Beta-defensins-2 and -3 in the upper and outer parts of the epidermis, particularly in the upper five or six layers of the *stratum corneum*. Lysozyme is found between the lamellae of the *stratum corneum*, in the cells of the *stratum spinosum,* free cells of the dermis, and in endothelial cells of dermal blood vessels. Beta-defensins (typically type 3) are clearly located in cells of the upper *stratum spinosum* and concentrated between the upper five or six layers of the *stratum corneum*. These compounds can occur extracellularly, and defensin production appears to be stimulated by invading microbes rather than being continuous as in the apocrine skin glands of haired marine mammals. The presence and distribution of these substances suggests that spotted dolphins possess a non-specific defense against bacteria, fungi, algae, and ectoparasites, despite the absence of typical skin glands such as those found in haired mammals, including pinnipeds (Myers and Seegers 2004).

Spotted dolphin skin can exhibit both "normal" and presumably stress-related "altered" chemical profiles, based on investigation of stress-responsive protein expression in skin samples collected from spotted dolphins at various anatomical and geographic locations, including from the jaws of dolphins killed in the tuna purse-seine fishery, the backs of bow-riding dolphins, and the dorsal fins and backs of animals captured and released during a research-seining project (Dizon et al. 2002)   While the concept is intriguing, it is not clear whether the "altered" profiles are related to the effects of fishing effort on skin chemistry. Further research will be required to determine the potential effects of various factors (e.g., skin sample location) on induction of the "altered" profiles, before the method can be used to practically assess stress effects in spotted dolphins.

The fat composition of the integumental blubber layer in spotted dolphins changes with age and differs from the composition of fats in the jaw and melon (Morii and Kanzu 1972). Oil from the blubber of spotted dolphin fetuses and nursing calves is much less saturated than the blubber oil of adults. In adults, iso-valeric is the most common short-chain fatty acid, but in fetuses and nursing calves, iso-butyeric or n-butyric acids are also abundant. Concentrations of iso-series branched chain fatty acids are very low in blubber oil of all ages. The jaw oil of adults and nursing calves, and the head oil of fetuses, contain abundant long-chain fatty acids (C_{10}-C_{22}) include many of the iso-series (Morii and Kanzu 1972).

Differences in fat composition of the head versus the blubber layer are probably related to differences in function, i.e., insulation by the blubber layer versus sound transmission by the head fats. Isovaleric acid (iso5:0) is an unusual fatty acid that is important for echolocation and hearing in acoustic tissues of some odontocetes, but its functional significance in blubber is unknown (Koopman et al. 2003). As in the other delphinids, the monodontids, and the phocoenids examined, iso5:0 accumulates in greater quantities (two to three times greater) in the superficial/outer blubber than in deep/inner blubber of the thorax, possibly related to a role in blubber flexibility (Koopman et al. 2003).

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MUSCLE SYSTEM

Although no complete analysis yet exists of muscle system form and function in spotted dolphins, a few studies address various aspects of this system. A series of sequential cross-sections through a frozen adult male specimen of *Stenella graffmani* (now renamed *Stenella attenuata*) illustrates, from head to flukes, various internal systems of the animal, including the musculature (Boice et al. 1964). Placements, relative sizes and composition of muscles and tendons of spotted dolphins appear to be very similar to those in other more commonly studied odontocetes such as *Tursiops truncatus* and *Dephinus delphis* (Pabst 1990, 1993, 1996a, b, 2000). Locomotion is accomplished through the actions of large muscles arranged along the axis of the vetebral column, which control the propulsive flukes. The pectoral and dorsal fins, as well as the head, have very limited motion, as in other odontoctes.

Structural adaptations contributing to hydrodynamic efficiency have been examined via detailed dissections of 5 odontocete species, including the spotted dolphin (Pabst 1996a). Like the other species studied, spotted dolphins possesses a complictated subdermal connective tissue sheath (a fiber-reinforced membrane connected to the vertebrae and various other locomotor tissues) and a complex system of intramuscular tendons which increase propulsive efficiency by various mechanisms (Rommel et al. 1993, Pabst 1996a, b). No other muscle systems have been examined in spotted dolphins.

NERVOUS SYSTEM

The cetacean nervous system, including that of spotted dolphins, has undergone significant adaptation to life underwater. Nervous system components important for aquatic survival tend to have increased in size relative to those in terrestrial mammals, while components related to relatively less important processes have decreased or disappeared (Oelschläger and Oelschläger 2009). For example, nerves responsible for movement of the relatively large cetacean head and propulsive tail are large, while nerves responsible for forelimb movement are relatively reduced. Nervous system structures associated with auditory processing, including structures relating acoustic and locomotor functions (e.g., medial trigeminal tract) are especially well-developed, reflecting the importance of acoustic signals for odontocete navigation, communication and foraging. In contrast, enervation of the cetacean visual system is reduced relative to that of the acoustic system (Oelschläger and Oelschläger 2009).

As in other odontocetes, the spotted dolphin brain is quite large (Perrin et al. 1977), with an extensive cortical surface area but a relatively thin cortex, about half that of humans, resulting in a cortical volume about 80% of human cortical volume (Ridgway 1986). In spotted dolphins, the whole brain is nearly or completely bilaterally symmetric, compared to slight asymmetry (slightly larger right hemisphere) in *Tursiops* and *Delphinus.* The neocortex is very densely folded and the generally globular shape is compressed from front to back due to the typical cetacean "telescoping" of the ancestral mammalian head (Boice et al. 1964, Oelschläger and Oelschläger 2009). Cortex surface area of spotted dolphin brain is about 1500 cm^2, somewhat less than that of *Delphinus*

sp. (about 2000 cm$^{2)}$ (Ridgway 1986)). The extreme folding of the neocortex produces the largest cortical surface area of any mammal (Oelschläger and Oelschläger 2009). Contrary to earlier impressions that the cetacean neocortex was relatively undifferentiated and homogeneous, more recent studies indicate considerable complexity (Hof et al. 2005, Oelschläger and Oelschläger 2009). The cortical complexity of the delphinid brain is reflected in relatively high encephalization quotients (EQ: brain weight/body weight) of approximately 3 to 4 (Ridgway 1986), similar to that in nonhuman primates (3.3) although substantially lower than the human EQ (7) (Hof et al. 2005). Cortical layering varies in complexity and thickness in various areas, as does neuron density; neuron volumes are about twice the maximal volume found in ungulates but still smaller than human neuronal volumes (Oelschlager and Oelschlager 2009). Despite lower neuronal density than in humans, cetacean synaptic density per unit volume and per neuron is much higher than found in terrestrial mammals, with the majority of synapses (70%) found in cortical layers I and II. As in other mammals, brain development is incomplete at birth in cetaceans, and continues during postpartum growth. For example, the glia/neuron ratio increases from birth to maturity, implying an important role for the glia in neuron growth and neocortical function (Oelschlager and Oelschlager 2009). Brain ganglioside composition of white matter and myelin (important for cellular recognition and cell-to-cell communication) in cerebrum and cerebellum of adult spotted dolphins is similar to that in *S. coeruleoalba*, as well as other Delphinidae, but ganglioside concentration in spotted dolphins tends to be lower than found in some other odontocetes and mysticetes, perhaps reflecting evolutionary differences (Terabayashi et al. 1990). The functional significance of these brain ganglioside patterns in unknown.

The acoustic-related nervous system in toothed whales, including spotted dolphins, is very highly adapted and developed. Nerve fiber systems indicate a nervous system circuit which integrates auditory input with locomotor activity, illustrating the importance of hearing in whale sensory systems (acousticomotor navigation) (Oelschläger and Oelschläger 2009). The auditory nerve is very large, exceeding even the trigeminal nerve (Boice et al. 1964). The importance of sound processing underwater presumably led to the observed hypertrophy of acoustic pathway nervous tissues and acoustic processing neocortical areas in odontodetes, including spotted dolphins (Oelschläger and Oelschläger 2009). Thalamus components related to auditory functions also tend to be quite large, although the usually–associated pineal organ tends to be reduced or even lacking in adult ceteceans. The functional significance of pineal reduction in cetaceans is unknown. The odontocete amygdala is well developed, as it is in bats, perhaps reflecting some function related to the complicated and extensive sonar system characteristic of odontocetes. Many nervous system structures related to auditory processing, e.g., the cochlear nerve and ventral cochlear nucleus, are larger in odontocetes than in mysticetes, perhaps reflecting a greater dependence on acoustic information in toothed whales. In contrast to most other acoustic system components, the vestibular nervous system in cetaceans is generally reduced, reflecting reduction in semicircular canals, with the exception of the Dieters' nucleus, a structure which appears to be strongly involved in acousticomotor navigation (Oelschläger and Oelschläger 2009).

The visual nervous system is only moderately well-developed in cetaceans, including spotted dolphins (Oelschläger and Oelschläger 2009). The optic nerves in spotted dolphins lie in an optic rete system consisting of many small arteries and veins, with the arteries more numerous (Boice et al. 1964). The walls of the veins are very thin with little muscle and the veins do not contain any valves, so blood appears able to flow in either direction. Another rete system, the cervical rete, surrounds the medulla oblongata in spotted dolphins (Boice et al. 1964). Presumably, these retes function to control temperature, oxygen, or the movement of other important factors in proximity to the adjacent organ.

Various other brain structures (e.g., the corpus callosum, the nucleus ellipticus, and the pituitary) also differ between cetaceans and terrestrial mammals. The corpus callosum provides a structural link between the two hemispheres of the mammalian brain, and can be considered an anatomical index of cerebral differentiation (Nieto et al. 1976). In most mammals, the surface area of a vertically-sectioned corpus callosum increases with increasing brain weight, but spotted dolphins differ in having a corpus callosum surface area similar to that of a horse, despite having a much heavier brain (Nieto et al. 1976). This reduction in relative size of the corpus callosum despite increasing brain weight is also found in other odontocetes (e.g., killer whales, Oelschlager and Oelschlager 2009). The relatively smaller corpus callosum in odontocetes may contribute to increased independence of the brain hemispheres, perhaps facilitating the observed ability of, for example, bottlenose dolphins to display electroencephalographic evidence of wakefulness in one hemisphere simultaneously with evidence of sleep in the opposite hemisphere (Oelschlager and Oelschlager 2009).

Spotted dolphins, like many other cetaceans and unlike most terrestrial mammals (except elephants), possesses a nucleus ellipticus in the mesencephalon (Nieto and Nieto 1984). This elliptical structure is large enough to be discerned without magnification, being a well delimited, compact nucleus with abundant neurons, surrounded by a band of fibrous tissues. The neurons of this strikingly large structure are unique in shape and different from any other type of neuron in the central nervous system (Nieto and Nieto 1984). This structure includes an area generally occupied by the red nucleus in other mammals and may correspond to the nucleus medialis anterior (Cozzi et al. 2000). The functional significance of this structure is undetermined but may be related to controlling movements in the blowhole region, and/or oculomotor movements (Nieto and Nieto 1984), given that analogous structures in other mammals appear to control facial muscles (Cozzi et al. 2000).

The spotted dolphin pituitary is similar to that of terrestrial mammals at the microscopic level, but differs macroscopically, being composed of "two distinct parts, the adenohypophysis and the neurohypohysis, which are separated by a thin fibrous membrane" (Cowan et al. 2008).   The pars intermedia and the hypophyseal cleft of terrestrial mammals are absent. As in other dolphins examined, the pituitary gland in spotted dolphins "is located at the base of the brain, close to the optic chiasm, on the

sphenoid bone". In spotted dolphins, unlike most other species, there is a well-formed deep sella instead of merely a shallow depression in the sphenoid bone. Pituitaries of spotted dolphins and the closely-related spinner dolphin (*Stenella longirostris)* are generally similar and sometimes contain colloid cysts, follicles, and/or mineralized bodies of unknown significance (Cowan et al. 2008). This organ presumably functions in cetaceans as it does in terrestrial mammals to regulate hormone activities via the endocrine system.

OLFACTORY SYSTEM

Like other cetaceans, spotted dolphins have a generally reduced olfactory system. They lack an olfactory nerve and therefore lack the ability to sense odors (are anosmic) (Nieto and Nieto 1986). Observed reduction in hippocampal and mammillary body size is likely related to this reduction in olfactory function although some chemoreception may remain in the oral cavity, in the absence of olfaction (Oelschlager and Oelschlager 2009).

The only study to examine olfactory morphology in spotted dolphins found Islets of Calleja consisting of many small, mainly pyramidal cells (Nieto and Nieto 1986). These structures are normal components of the olfactory system in terrestrial mammals and consist of clearly recognizable small and medium sized pyramidal cells located in the olfactory tubercle. Some Islets of Calleja in spotted dolphins also contained numerous small polygonal cells with several dendritic projections containing abundant dendritic spines and a lone thin axon, probably representing a dense area of connectivity in a region that is also heavily vasularized. Because earlier research had determined that, despite being anosmic, dolphins retain other ancillary components of the usual olfactory system, including the amygdala, hippocampus, septum, and habenula (while lacking the pineal gland with which the habenula is usually associated), there may be an alternative function for the Islets of Calleja as part of the limbic and paralimbic systems (brain structures that are involved in emotion processing, goal seeking, motivation and self-control in humans)perhaps involving emotional behavior (Nieto and Nieto 1986), although this suggestion has yet to be investigated in spotted dolphins.

REPRODUCTIVE SYSTEM

Reproductive Parameters.   Reproductive parameters of spotted dolphins have been studied in two different management stocks in the eastern tropical Pacific Ocean (related to the tuna purse-seine fishery; northern offshore and southern offshore spotted dolphins, Perrin et al. 1985) and near Japan (Kasuya 1985).   Estimated average lengthat sexual maturity in male spotted dolphins in the eastern tropical Pacific Ocean is about 195 cm, compared to about 181 in females (Perrin et al. 1976). Average age at sexual maturity is 12-15 years in male spotted dolphins (Hohn et al. 1985, Perrin 2009) and 9-11 years in females (Kasuya et al. 1974, Kasuya 1976, Myrick et al. 1986, Perrin 2009); the range for females is 9-17 years (Perrin et al. 1987) though there is a marked differences between populations, especially within the ETP. Consistent with the differences in length at sexually maturity, female northern offshore spotted dolphins mature on average

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significantly later (11.1 years; SE=0.236, n=520) than southern offshore spotted dolphins (9.8 years; SE = 0.264, n=403) (Chivers and Myrick 1993).

Annual pregnancy rate, i.e., the proportion of sexually mature females that are pregnant divided by gestation time (expressed in years), varies by population between 0.25- 0.4. In the ETP, chase and encirclement by the purse-seine tuna fishery may affect pregnancy rate; highest rates occur in areas of relatively low fishery effort (Kellar 2008). Gestation has been estimated to be 11.2-11.5 months (Harrison 1969, Kasuya et al. 1974, Perrin et al. 1976), though ontogenetic evidence suggests that it may be shorter (9-10 months) (Štěrba et al. 2000). Pregnancies have been observed in ETP spotted dolphins up to 35 years of age (Myrick et al. 1986). Aged females may become post-reproductive, though if so, it is uncommon (< 1% of mature females) (Perrin et al. 1976, Myrick et al. 1986). Average calving interval in the eastern Pacific appears to be 2-3 years and in the western Pacific 4-6 years, with the difference possibly related to differential status of the populations (Kasuya 1985, Myrick et al. 1986, Perrin 2001, 2009); the eastern Pacific populations have been significantly depleted compared to pre-fishery population levels (Smith 1983, Wade et al. 2007) while the western Pacific population is relatively unexploited.   These estimated calving intervals assume that no prenatal mortality occurs, and therefore are likely to be underestimates.

Estimated length at birth is 80-85 cm, being slightly greater in northern offshore spotted dolphins than in southern offshore spotted dolphins (Kasuya et al. 1974, Perrin et al. 1977, Hohn and Hammond 1985, Perrin et al. 1985, Perrin 2009). Average duration of lactation is 1–2 years and varies with population, being shorter in the eastern tropical Pacific than in the western Pacific (Myrick et al. 1986, Perrin 2001, Archer and Robertson 2004). The average age and length at weaning are approximately 9 months and 122 cm, although nursing can continue to about 2 years of age (Archer and Robertson 2004). About 10% of lactating females are also pregnant in the ETP (Perrin et al. 1976). Estimated gross annual production of calves in the eastern topical Pacific Ocean is about 14% per year (based on the age and sex structure of sampled dolphins and an estimated average pregnancy rate of 0.469, Perrin et al. 1976), although again, prenatal mortality has been assumed nil, so conception rate may be underestimated. This production rate may be decreased by exposure to tuna purse-seine activity (Cramer et al. 2008). Reproduction appears to be somewhat seasonal in the eastern tropical Pacific, especially for the southern offshore spotted dolphin which appears to have a fairly well defined calving peak late fall/early winter, while the northern offshore population has 2–3 weakly defined calving seasons in fall, spring, and possibly summer (Perrin et al. 1976, Hohn et al. 1985, Hohn and Hammond 1985). Testis and epididymis weights peak in April for the southern offshore spotted dolphin and peak weakly in July and August, midway between the two predicted mating seasons for northern offshore spotted dolphins, but spermatozoa levels tend to be elevated during the predicted breeding season (i.e. late fall and spring) (Hohn et al. 1985).

Reproductive Morphology of the male. Testis mass of spotted dolphins is similar to that of other dolphins and is much higher than testis mass in most other mammals (7-25 times larger than predicted for their body mass (Harrison 1969, Kenagy and Trombulak 1986). The testes are internal, and male spotted dolphins probably have morphological adaptations for cooling similar to those observed in *Tursiops truncatus*. In *Tursiops truncatus*, a vascular counter-current heat exchanger (CCHE) cools the intra-abdominal testes through juxtaposition of spermatic arteries in the poster abdomen, with veins returning cooled blood from the surfaces of the dorsal fin and tail flukes. Vigorous swimming leads to decreased temperature at the CCHE relative to resting and pre-swim values, implying that the CCHE increases in cooling ability with exercise (Pabst et al. 1995).

Reproductive Hormones (male). Reproductive hormone levels in males have been reported from analysis of blood collected from 4 male spotted dolphins within two hours of death due to purse-seine operations in the ETP (Sawyer-Steffen and Kirby 1980). Testosterone values below 1 ng ml^{-1} were assumed to indicate immaturity, while values above 4 ng ml^{-1} were assumed mature. In the two immature males, seminiferous tubule diameters were 10.1 and 12.9 microns, testosterone levels were 0.340 and 0.87 ng ml^{-1}, left testis weights were 7 g and 9 g, and total body lengths were 176 and 172 cm. In the two mature males, seminiferous tubule diameters were 43.1 and 36.2 microns, testosterone levels were 4.43 and 6.56 ng ml^{-1}, left testis weights were 418 g and 1 26 g, and total body lengths were 195 and 191 cm. These testis weights and body lengths are consistent with earlier measurements by Hohn et al. 1985. Hormone analyses of blood taken from 4 living male spotted dolphins during a chase and capture experiment in the ETP found an average testosterone level of 5.5 ng ml^{-1}, ranging from 0.02 to 35 ng ml^{-1} (St. Aubin et al. 2011).

Reproductive Morphology of the female. Ovulation tends to begin in the left ovary, which becomes much larger than the right ovary during most reproductive years. In older animals, the right ovary becomes dominant but ovulates rarely (Ohsumi 1964, Arvy 1977b). Corpora tend to be much more numerous in the left than the right ovary, similar to the pattern found in *Tursiops truncatus, Delphinus delphis, Stenella coeruleoalba,* and *Langenorhynchus obliquidens* (Arvy 1977b). The corpora lutea (CL) of spotted dolphins, like other small delphinids, are massive relative to overall ovary size when compared to other mammals (Dabin et al. 2008, Kellar 2008). The mass of ovaries with CLs are on the order of seven times greater than those without CLs.

Female spotted dolphins probably have morphological adaptations for cooling the uterus, similar to those observed in other cetaceans. In all examined cetacean species, female reproductive morphology includes vascular plexuses associated with the uterus (Rommel et al. 1993). The plexuses create a complex countercurrent heat exchange system that likely regulates the thermal environment of the uterus and developing fetus. A lumbo-caudal venous plexus takes in cooled blood from the surfaces of the flukes and dorsal fin, acting as a heat sink by being juxtaposed to arterial and venous plexuses associated with the uterus. The plexuses appear to form a counter-current heat exchanger

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similar to that found in male cetaceans (Rommel et al. 1992), so that cool superficial blood is introduced into the insulated abdominal core, allowing heat to be transferred away from the reproductive organs.

Reproductive Hormones (female).   Reproductive hormone levels in female *Stenella* spp. have been reported from analysis of blood collected from 2 female spotted dolphins and 4 female *Stenella longirostris* within two hours of death due purse-seine operations in the ETP (Sawyer-Steffen and Kirby 1980). Of the six female *Stenella* spp., 3 were judged immature through histological examination and had an average progesterone level of 1250 ± 29 ng ml^{-1}. The three remaining females were mature: one resting (neither pregnant or lactating, with no active CL), one lactating, and one pregnant.   Only the pregnant female had a progesterone level above that of the immature females, at 7607 ng ml^{-1}. These levels are similar to those measured in *Tursiops truncatus* in captivity.   In captive *Tursiops*, normal baseline progesterone is about 300 ng ml^{-1}, rising tenfold after ovulation to over 3000 ng ml^{-1}, and remaining elevated above 4000 ng ml^{-1} during pregnancy. Progesterone levels in the blubber tissue of spotted dolphins show larger differences between pregnancy states; mean values from pregnant females are approximately 50 times greater than those for non-pregnant females (6.8 ng g^{-1}) (Kellar 2008).

Ovulation. The presumed ovulation rate estimated from counts of *corpora albicantia* (CA) for adult female spotted dolphins is 0.4–0.6 ovulations per year in the ETP, is highly variable among individuals, and appears to slow abruptly after about 8 ovulations (Myrick et al. 1986, Perrin 2001). Ovulation rate decreased from about 4 apparent ovulations per year in very young females to about one per year in older females (Myrick et al. 1986). A small number of females (<1%) appear to survive while reproductively senescent in the ETP (Myrick et al. 1986). However, several recent studies have indicated that interpretating rate of CA acquisition may be more complex than previously thought. A study of *Delphinus delphis* indicates that CAs are unlikely to represent a direct record of past ovulations (Dabin et al. 2008). Ultrasonography studies tracking ovary changes in *Tursiops aduncus* suggest that persistent CAs are derived from CLs of pregnancies, which are larger than those of ovulation (Brook et al. 2002).   Recent histological work in *Delphinus delphis* indicate there are two types of CAs, one with lots of elastin (more persistent) and one without (less persistent) (Takahashi et al. 2006). Taken together these studies indicate that CAs represent a combination of all (or nearly all) past pregnancies and more recent past ovulations.

Dolphins are usually assumed to be reflex (induced) ovulators, similar to camelids. However, also similar to camelids, spontaneous ovulation may sometimes occur. Prevalence of spontaneous ovulation was investigated in spotted dolphins from the ETP through examination of 58 apparently non-pregnant uteri and ovaries of *Stenella longirostris* and spotted dolphins which nevertheless contained CLs, with special attention being paid to reasons for the presence of these CLs, such as early undetected pregnancy (Benirschke et al. 1980). The non-pregnant organs were compared with control specimens of immature, pregnant, and lactating females. Previous studies had

shown that 5% of spotted dolphin specimens with CLs were non pregnant and 2.8% of *Stenella longirostris* with CLs were neither pregnant, lactating, nor post-abortion. Although the Benirschke et al. (1980) study results indicated that 20-30% of these cases were misdiagnosed and were CLs degenerating rather than maintaining pregnancy, there was sufficient evidence that spontaneous ovulation does occur, although probably infrequently, in spotted dolphins. Additional evidence from sonography/endocrine analysis in captive animals has confirmed these findings (Robeck 1996, Brook 2001). Distinguishing between spontaneous versus reflex ovulation in free-ranging animals may be difficult: under normal conditions, the copulation rate may be frequent enough in these schooling animals that the vast majority of ovulations are fertilized irrespective of their initiation mechanism. It should be noted that in captive delphinids there is evidence that functional CLs can persist in the absence of a developing embryo or fetus. The cause of this condition, pseudopregnancy, in cetaceans is unknown but it is often associated with early term abortion or females without access to males for extended periods (Robeck et al. 2001). The rate of pseudopregnancy in spotted dolphins is unknown but may contribute to the number of CLs not associated with embryo or fetus.

Placenta. The vast majority of spotted dolphin uterine implantations, like those of other delphinids, occur in the left horn with ipsolateral CL development, for reasons not yet understood. The delphinid placenta is a very thin, villi covered, diffuse, epitheliochorial organ (Slijper 1966). There is no placental invasion into the endometrium; instead the villi tenuously interdigitate with the endometrial glands. As such the placental membranes develop quickly, beoming quite large early in developement, ultimately explanding into both urine horns, leaving very small embryos enclosed in expansive membranes (Benirschke et al. 1980). Urine is carried out from the urachus to a huge allantoic sac through a large allantoic duct (Slijper 1966). Circulation through the umbilical cord is achieved via 4 major vessels (2 arteries and 2 veins) branching out as they extend toward the placental periphery and the fetal/maternal barrier (Slijper 1966, Benirschke and Cornell 1987).

Milk Composition. Spotted dolphin milk fat content is much lower than that of baleen whales but higher than that of other dolphins (20-25% lipid) (Pilson and Waller 1970, Morii 1981). Composition did not appear to change during the course of lactation in a sample of 8 spotted dolphins (188-205cm total length) killed during tuna purse-seine operations in the ETP (Pilson and Waller 1970). Lactose is the primary milk sugar, in similar concentration to milk of other cetaceans. Chloride concentration is elevated relative to cows, presumably so that osmotic pressure of the milk remains similar to that of the blood in the dolphin's saline environment (Pilson and Waller 1970). Spotted dolphin milk contains a number of long- and short-chain fatty acids, both free and in milk lipids, which are subsequently incorporated into body tissues of nursing calves (Morii 1981).

RESPIRATORY SYSTEM

In general, cetacean lungs are adapted for their aquatic habitat via large tidal volumes (6-10% of total body volume, compared to about 5% in humans), a flexible

chest cavity with mostly floating (unattached) ribs, and terminal airways lined with cartilaginous structures that prevent lung collapse at low lung volumes (Kooyman and Sinnett 1979, Ridgway and Harrison 1986). As in most delphinids, the terminal airways of the lungs in spotted dolphins contain well-developed serial sphincter muscles (Kooyman and Sinnett 1979). These adaptations allow dolphins to complete a respiratory cycle in 0.2-0.3 s, and achieve peak flow rates of about $0.6 \text{ L s}^{-1} \text{ kg}^{-1}$ (4 times greater than in humans) (Kooyman and Cornell 1981), as observed in free-ranging spotted dolphins in the ETP (Hui 1989). These spotted dolphins were observed to ventilate at slow speeds by rolling at the surface, at intermediate speeds by partially leaping, and at high speeds by leaping completely out of the water (Hui 1989). During these observations, blowhole exposure time also increased with water surface roughness and with the need to accomplish multiple breaths per exposure. At high swim speeds, during which the dolphins swam about 13 m between leaps, exposure time was maximized by increasing the angle of emergence from about 30° to 37°. Blowhole exposure times during moderately active swimming and quasi-leaps (about 2.5 body lengths s^{-1}) was about 0.37 s (s.d. 0.03), increasing during full-leap swimming to about 0.56 s (s.d. 0.085). During bow-riding, inhalation time was about 0.18 s (s.d. 0.062) and exhalation time was about 0.26 s (s.d 0.006) (Hui 1989), probably reflecting energy savings during this swimming mode.

On a histological level, spotted dolphin lungs (2 female, 1 male; 1 adult, 2 immature, collected during fishing activities around Japan) have been found to contain pulmonary intravascular macrophages (PIMs), similar to 41 other species of odontocetes examined (Kawashima et al. 2004a). PIMS are also found in ungulates, horses and burros, and cats. These macrophages remove by absorption, blood pathogens such as bacteria, endotoxins, aged erythrocytes, and cellular debris as well as air-borne, aspirated foreign bodies. They then transfer the pathogens to neighboring lymph nodes through lymphoid vessels. Distribution and morphology of PIMs in the cetaceans examined were similar to PIMs in terrestrial animals and were not associated with any disease conditions known to induce PIMs in other animals, indicating that cetacean lungs routinely contain PIMs under physiologic conditions. Although helpful in removal of inhaled pathogens from the lungs, the presence of pulmonary PIMs in cetaceans may also contribute to the prevalence of bacterial infections observed in these animals. Animals having PIMs show higher sensitivity of the lungs to gram-negative bacterium-derived endotoxins, probably due to induction of acute lung injury resulting in release of imflammatory mediators. Pulmonary disorders caused by primary or secondary bacterial infection are relatively common in small cetaceans, with a number of fatal gram-negative bacteria having been isolated from septicemia (Kawashima et al. 2004a). PIMs may therefore play an important role in the induction and progression of fatal infections in cetacean lung diseases, although this has not been demonstrated to date in spotted dolphins.

SKELETAL SYSTEM

Studies of skeletal characteristics in spotted dolphins have focused on tooth structure and skull morphology because age estimation and stock (population) identification are important for management (e.g., Wade et al. 2007).

Age estimation based on tooth structure. Two methods have been used to examine spotted dolphin teeth for age-related changes that might provide information about size–at-age and reproductive status. The first method examined tooth structure for the presence of recurring patterns similar to tree rings ((Myrick 1980b, a, Myrick et al. 1983, Klevezal and Myrick 1984). The second method examined amino acid racemization in dentine and eye lens material from a sample of non-aged spotted dolphins and a sample of 14 "tooth-aged" spotted dolphins, to determine whether racemization rate might be useful as a proxy for age (Bada and Brown 1981). The tooth structure studies proved significantly more rewarding that the racemization study. The ratio of aspactic acid racemization rates in dentine and lens proteins (D/L aspartic acid ratio) for spotted dolphins was 0.20, (vs. 0.63 in man, 0.23 in northern fur seal, and 0.24 in white whale, Bada and Brown 1981). In the sample of 14 spotted dolphins ranging in "tooth age" from 0.8 to 23 years, D/L aspartic acid ratio varied from 0.1 to 0.8, and aspartic acid age ranged from 0 to 12 years, with little correspondence between tooth ages and aspartic acid ages (Bada and Brown 1981).

Examination of tooth structure in spotted dolphins revealed growth layer groups (GLGs) resulting from incremental variation in deposition of the mineral hydroxyapatite in dental and periosteal tissues (Myrick 1980a). During growth, crystal lattices of hydroxyapatite are deposited in orientations that differ from increment to increment but have a common alignment within a given growth segment. Polarized light shining through decalcified and stained thin sections of teeth makes visible these growth-related variations in alignment, which appear as lines across the sections (Myrick 1980a).

In spotted dolphins, GLGs form in both dentine and cementum (Myrick et al. 1983). Both dentinal and cemental GLGs contain lightly stained and darkly stained layers, but the size and thickness of the layers differs between the types. *Dentinal* GLGs are composed of two thin lightly stained layers and two thicker darkly stained layers, and are the primary source of age estimation. *Cemental* GLGs are composed of one lightly stained layer and one darkly stained layer (Myrick et al. 1983).

The basic pattern of dentinal tissue distribution and deposition is common to all delphinids (Myrick et al. 1983). Teeth in new-born dolphins consist of a thin, external, conical mantle of enamel covering a thicker, basally-tapered cone of *prenatal* dentine and part of a thin, inner, layered cone of *neonatal* dentine. These internally-nested cones surround a central pulp cavity. The neonatal cone produces an obvious neonatal line in thin section (Myrick 1980b). This neonatal line is first in a series of internally-deposited, layered cones comprising the GLGs observed in postnatal dentine (Myrick et al. 1983). The number of GLGs observed in a given tooth depends upon the age and deposition rate of the dolphin sampled (Myrick et al. 1983). In spotted dolphins, as in other species examined, it appears that one GLG generally corresponds to one year postpartum, although other deposition patterns may occur (Myrick et al. 1984, Hohn et al. 1989, Hohn 2009). As a dolphin matures and dentine continues to accumulate, pulp cavity volume decreases and successive GLGs become thinner (Myrick et al. 1983). In the late-formed

dentine of older dolphins, GLGs become increasingly irregular and difficult to distinguish. In these older animals, cementum layers may provide a more accurate age determination (Myrick et al. 1983).

Cementum is deposited only postnatally (Myrick et al. 1983). Cementum is applied to the external surface of the root in concentric layers, below the neck of the tooth. Because cementum deposition is external and apparently unconfined, it is thought to form a continuous record representing a dolphin's entire postnatal life. Unlike the dentinal GLGs, the cementum GLGs do not display a regular or uniform thickness. The number of dentinal and cemental GLGs is usually, but not always, the same in a given dolphin. Cementum GLGs occur in multiples in some teeth, while in other layers it may be thin with no distinct layering or with only half the number of GLGs observed in the dentine. Therefore, cementum may be used to estimate maximum ages of older dolphins only if a relationship between cemental and dentinal GLGs can be established from the younger regions of the tooth (Myrick et al. 1983).

Tooth structure of adult spotted dolphins contains up to 240 striae in the prenatal *enamel*, perhaps indicating daily cycles, and about 60 incremental layers in the prenatal *dentine*, of unknown significance (Myrick 1980b). The postnatal *dentine* contains 13 regularly-spaced accessory layers in the first five or six GLGs, with each accessory layer containing an average of 28 microlayers. Accessory layers may reflect lunar (monthly) cycles, while the microlayers may reflect daily cycles.   Fewer accessory layers are evident in cementum GLGs than in dentinal GLGs. GLGs in periosteal bone consist of accessory layers that also may reflect lunar cycles. Observed layering patterns in dentinal, cemental, and perisoteal tissues may result from the same cyclic influences (Myrick 1980b).

Sexually mature spotted dolphins often exhibit a prominent dark-stained, relatively thin layer (dsl) at the boundary of one or more of their annual growth layer groups (Klevezal and Myrick 1984). Dsls are found in teeth from both male and female spotted dolphins, although they tend to be less distinct and less common in males than females. Dsls have been found in all female teeth examined but in only about half to a third of males examined. Although no explanation exists for the presence of dsls in males, the number of dsls in female spotted dolphins appears to correlate with birthing history, so the number of dsls may indicate the minimum number of calf births. Dsls were found in the last or next to last GLG of teeth from 35 of 40 lactating female spotted dolphins.   Dsls found in 17 of 35 non-lactating females (both pregnant and non-pregnant) were assumed to result from calves lost subsequent to parturition, so that lactation had begun but ceased prior to collection of the teeth. Although prominent dsls are relatively uncommon in teeth from male spotted dolphins examined, most do contain a less distinct dark-stained boundary layer, in the eighth or nineth GLG. A similar less distinct layer has also been observed in teeth from most female spotted dolphins examined, in the sixth or seventh GLG. Assuming GLGs indicate annual growth, these less distinct dsls are occurring about three years prior to puberty in both males and

females, and therefore may be related in some way to the maturation process (Klevezal and Myrick 1984).

Stock identification based on skull morphology. The spotted dolphin skull is 35–46 cm long in adults (Perrin 2001). The long narrow rostrum has no palatal grooves, 35–50 teeth in each row, medium–sized rounded temporal fossae, convergent premaxillae, and arcuate mandibles. Various aspects of spotted dolphin skull morphology have been examined in relationship to body length, environmental variables, gender, and geographic location in order to elucidate and define the presence and distribution of various stocks of spotted dolphins in the ETP (Perrin 1975a, Perrin et al. 1979, Schnell et al. 1982, Douglas et al. 1984, Perrin et al. 1985, Schnell et al. 1985b, a, 1986, Perrin et al. 1987, Perrin et al. 1991, 1994) and in the western tropical Pacific Ocean near Japan and Taiwan (Yao et al. 2008). Studies in the ETP have found that statistically significant sexual dimorphism occurs in about 65%, and geographic variation occurs in almost all, spotted dolphin skull morphometrics in this area (Perrin et al. 1991), but little or no seasonal variation occurs within localities (Schnell et al. 1982).

Sexually dimorphic skull characteristics in ETP spotted dolphins include braincase, feeding apparatus, and postcranial elements (Perrin 1975a), with differences ranging from 1% to 6% (Schnell et al. 1985a). In general, rostrum and ramus are longer in females, while most other skull characteristics are larger in males (Schnell et al. 1982, 1985b, Perrin et al. 1991, Sanvicente-Anorve et al. 2004). In contrast, the rostrum is wider and more robust in male than in female spotted dolphins in the western Pacific (Yao et al. 2008). In addition, female spotted dolphins from Japan and Taiwan were more similar to each other than to female dolphins from the ETP (Yao et al. 2008).

In the ETP, spotted dolphin skull morphometrics vary substantially along north-south and inshore-offshore geographic clines (Schnell et al. 1982); the most influential skull characters are preorbital and temporal fossa widths (Schnell et al. 1985a). These clinal variations in morphology mirror trends found in a number of environmental variables: water depth, solar insulation (January), sea surface temperature (January and July), surface salinity, and thermocline depth (winter and summer) (Schnell et al. 1986, Perrin et al. 1991). The strongly clinal geographic patterns in both cranial morphology and environmental variables imply that oceanographic conditions may partially explain trends in morphological characteristics of spotted dolphins (Schnell et al. 1986). Covariation between skull morphology and environment is strongest for measures that vary north to south (e.g., solar insolation, salinity, and depth of the oxygen minimum layer) (Schnell et al. 1982). The especially strong differences in cranial morphology found between northeastern and western/southern types of spotted dolphins implies restricted gene flow and separate management units, supporting recognition of western/southern spotted dolphins as a separate stock (Schnell et al. 1986, Perrin et al. 1991).

Coastal spotted dolphins (*S. a. graffmani*) are especially distinctive (Perrin et al. 1991). They occupy near-shore coastal waters and have substantially larger skulls, a less

attenuated rostrum, and wider, but fewer, teeth than the offshore form. Tooth width is the most distinctive character differentiating inshore and offshore specimens. Differences in some skull characters between northern vs. southern areas are also found *within* groups of specimens collected from particular locations (Schnell et al. 1982). For example, spotted dolphin skulls from southern offshore locations are more robust and wider than those from northern offshore locations, except for the temporal fossa, which tends to be smaller in southern spotted dolphins (Perrin et al. 1985).

Similarities in skull morphology of spotted dolphins from far western (including around the Hawaiian Islands) and southern offshore areas (Schnell et al. 1982, Schnell et al. 1986) have led to spotted dolphins west of 120°W being pooled with southern spotted dolphins, rather than with those from northeastern areas, and to a north-south boundary definition at 5°N (Perrin et al.1991). The similarity between southern and (north) western spotted dolphins, rather than between northeastern and northwestern spotted dolphins, suggests a generally concentric pattern of geographic variation similar to that found for *Stenella longirostris* (Perrin et al. 1991).

URINARY SYSTEM

Like other cetaceans and pinnipeds, and in contrast to terrestrial mammals, spotted dolphins possess a reniculate kidney. This specialized kidney reflects their saline aquatic environment, and is adapted to process the large amount of electrolytes and water ingested with their marine fish and invertebrate prey. Unlike pinnipeds, the cetacean kidney (including that of spotted dolphins) possesses a *sporta perimedullaris musculosa* (an intra-renicular basketwork peculiar to cetaceans) (Cave and Aumonier 1965). "The cetacean kidney is a characteristically composite organ, comprising an associated multitude of reniculi or miniature kidneys, each of which displays a single medullary pyramid, a single calyx, and an independent blood supply. " …likened to a cluster of grapes, wherein each grape is a reniculus and the supportive stalk of the bunch is the mesenteric system" (Cave and Aumonier 1965). Unlike most other mammals, the fibromuscular tissue of the calyx wall doesn't terminate abruptly at the cortico-medullary junction.   Instead, this tissue extends into the reniculus interior in a basketlike form, circumscribing the medullar tissue (Cave and Aumonier 1965).

In some other aspects, spotted dolphins kidneys differ from those of other cetaceans (Cave and Aumonier 1965). In spotted dolphins, the reniculus (and the relative volume of medullary tissue) is relatively uniform, and the renicular cortex encroaches very markedly on the calyx and infundibular wall. The calyx in spotted dolphins penetrates much more deeply than in other cetaceans examined, and because the size and extent of the sporta depends on the degree of calyx penetration, the sporta of spotted dolphins is relatively restricted.   The sporta in spotted dolphins includes 6 strands in a combination of broad and narrow strips. The plain muscle content of the strips is notably abundant in spotted dolphins, the most of any cetacean studied.   Due to the extraordinarily deep penetration of the calyx, the radial veins in spotted dolphins are unusually short. At present, the functional significance of these characteristics is unknown (Cave and Aumonier 1965).

Renal function and blood chemistry of spotted dolphins are more similar to those of other marine cetaceans than to those of land mammals, reflecting adaptation to their marine habitat and exhibiting elevated plasma osmolality, sodium concentration, urea concentration, and hematocrit (Malvin and Rayner 1968). Oxygen isotope composition of tooth phosphate in spotted dolphins strongly indicates ingestion of sea water rather than fresh water during tooth deposition (Thewissen et al. 1996). No differences have been found among the cetacean species with regard to any plasma values. Values specific to spotted dolphins included: about 4.5 mEq l^{-1} K (vs. mean of 4.2 in other cetaceans, sd. 0.39), about 18.5 millimoles l^{-1} Urea (vs. mean of 16.6, s.d. 1.91), osmolality of 346 milliosmoles kg^{-1} water (vs. mean of 341, s.d. 7.3), about 128 mg $100ml^{-1}$ glucose (vs. mean of 117, s.d. 17.8), hematocrit of about 0.54 (vs. mean of 0.56, s.d. 0.021), and packed red blood cell values of 28.8, 81, and 57 mEq l^{-1} for Na, K and Cl, respectively (vs. means of 20.1 (s.d. 1.9), 90 (s.d. 11), and 50 (s.d. 5), respectively) (Malvin and Rayner 1968). Concentrations of sodium and the kidney enzyme renin (renin helps to control the body's sodium-potassium balance) in plasma of spotted dolphins is similar between animals, similar to those in the other cetaceans tested, and similar to values reported for other mammals, with no apparent differences due cetacean's seawater habitat (Malvin and Vander 1967).

Clearance experiments (which examine the time course of urine components following a meal) utilizing intravenous infusions, urine collection from the bladder, and blood sampling found that after a meal of fish, urine flow, GFR (glomerular filtration rate) and RPF (renal plasma flow) all increased (Malvin and Rayner 1968). After 6 hours, GFR and RPF decreased to minimal values but urine flow remained elevated. Urine osmolality remained high regardless of a more than 25-fold increase in urine flow rate (Malvin and Rayner 1968). Mechanisms controlling urine flow remain unclear.

VISUAL SYSTEM

The cetacean eye is adapted for light sensitivity, and visual pigments in spotted dolphins are similar to those of several other cetaceans, being homogeneous and based exclusively on a single retinal pigment, retinal-1, a type of rhodopsin (McFarland 1971). It is likely that spotted dolphins lack functional short-wavelength-sensitive (SWS) cone pigment, as has been found for many other cetaceans (Levenson and Dizon 2003). Absence of this pigment may serve to reduce sensitivity to easily-scattered short-wavelength light and increase visibility of long-wavelength targets, as an adaptation to the low-light conditions characteristic of underwater environments (Levenson and Dizon 2003). As in other cetacean eyes, the spotted dolphin eye is dominated by rods interspersed with relatively scarce modified "cone-like" structures and a reflective tapetum fibrosum that blankets the entire retinal surface, maximizing light capture (McFarland 1971). These adaptations are consistent with the dim, predominately blue to blue-green light conditions characteristic of the upper 100 meters of the oceanic water column.

In general, visual pigments of delphinds are very similar between species with each probably containing the same blue-sensitive rhodopsin (VP486$_1$) (McFarland 1971). Blue-shifted eye pigments are found also in many marine fishes, probably as an adaptation to improve detection of bioluminescent prey, which tend to emit blue-shifted light. Delphinid absorption maxima, including those of spotted dolphins, tend to cluster around 485 nm (McFarland 1971, Table 1) conveniently coinciding with the 470-490 nm emission range of many bioluminescent organisms (McFarland 1971). This is likely helpful for spotted dolphins which forage primarily at night on mesopelagic prey (myctophid lanternfishes and squid) rising from the deep scattering layer nocturnally (Scott and Chivers 2009).

EXTERNAL CHARACTERISTICS

General Characteristics. Information regarding body dimensions, external coloration, geographic variation, similarities to other dolphins, ecology (including parasites and predators), behavior and life history of the pantropical spotted dolphin is summarized through the mid-1980s in Perrin et al. (1987), the definitive source presenting a revision of the spotted dolphins, *Stenella* spp. Perrin et al. (1987) also discuss similarities and differences between spotted dolphins and other small delphinids including S. *frontalis, S. longirostris, S. clymene, S. coeruleoalba, Delphinus delphis, Lagenordelphis hosei*, and *Tursiops truncatus.* A general summary of current information on various aspects of spotted dolphins appears in Perrin (2009).

Spotted dolphins occur worldwide in tropical and some subtropical waters, from approximately 30-40°N to 20-40°S (Perrin 2009), with individuals occasionally found in colder waters (e.g. Alaska (Perrin et al. 1987)) and Santa Cruz, CA (Worthy et al. 1993). In general, spotted dolphins can be identified externally by the long beak sharply demarcated from the melon, slender body, strongly falcate dorsal fin and in adults, spots (Perrin 2009). Body color changes significantly between birth and adulthood (see Postnatal Development).

Geographic variation in external characteristics. Degree of spotting and body length of spotted dolphins both vary geographically. For example, both sexes of coastal Pacific spotted dolphin (*Stenella attenuata graffmani*) are on average more heavily spotted than the pantropical form (*Stenella attenuata)* in the offshore eastern tropical Pacific Ocean (Perrin et al. 1987). Both sexes also tend to be somewhat longer inshore and north, compared to offshore and south. For example, coastal spotted dolphins in the ETP, the coastal western North Atlantic, and the Gulf of Mexico tend to be larger than offshore spotted dolphins in the ETP and around St. Helena in the Atlantic (Perrin et al. 1987). Specifically in the eastern Pacific, coastal adult male spotted dolphins found from northern Mexico to Equador tend to average about 23 cm longer than offshore adult males, while coastal adult female spotted dolphins average about 19 cm longer than offshore adult females (Perrin et al. 1985).

Sexual dimorphism in external characteristics. Adult pantropical spotted dolphins are sexually dimorphic in body length (Perrin and Reilly 1984, Perrin et al. 1987, Perrin and

Hohn 1994). In general, males tend to be slightly larger than females in body size and most skull characters (Perrin 2009). Males tend to be longer than females in any given geographic area (Schnell et al. 1982). Male lengths range from about 165-255 cm; female lengths range from about 160-240 cm, with some patterns of geographic variation evident (Perrin et al. 1987). In the eastern Pacific, average lengths of adult males in the coastal and offshore subspecies are 223 cm and 200 cm, respectively, while average lengths of adult females are 207 cm and 182 cm, respectively. Male lengths in the western North Pacific, southwest Indian Ocean, North Atlantic, and Gulf of Mexico range from 193 to 234 cm; female lengths in these areas range from 173 to 215 cm. Modal size of male spotted dolphins from the eastern portion of the "northern offshore" range in the ETP is about 3.5 cm longer than that of males from the "southern offshore" region; the difference for females is about 2.5 cm (Perrin et al. 1985). Differences are smaller west of 120°N: 2.0 cm for males, 1.3 cm for females.

External Asymmetry. Moderate asymmetry of the flukes occurs in spotted dolphins. The left side of the fluke can be larger than the right side, as in *Stenella coeruleoalba, Delphinapterus leucus* and*Tursiops truncatus* (Arvy 1977a). The differences are slight and appear more as a greater curvature of the right side leading edge compared to the left side, perhaps assisting during turning or rotary motions (Arvy 1977a).

HYDRODYNAMICS

The external morphology of spotted dolphins is typical of delphinid cetaceans (Boice *et al*. 1964), being highly adapted to reduce hydrodynamic drag. Body shape is roughly cylindrical, tapering at both ends, and pierced by relatively small, firm smooth projections (rostrum, dorsal and pectoral fins, and flukes). The integument of spotted dolphins, together with its underlying morphology, creates the hydrodynamic surface that controls the energy cost of swimming. Swim performance of spotted dolphins has been examined under theoretical, experimental and *in situ* conditions. Theoretical models estimating swim performance of spotted dolphins are based on the observation that dolphin swimming is thunniform (Webb 1975), with the exception that power is provided by a vertically rather than horizontally oscillating hydrofoil (tail flukes, in dolphins), so that models developed for swimming tuna can be adapted for swimming spotted dolphins (Edwards 1992, 2002, 2006). Because model estimates tend to correlate relatively well with empirical measurements on spotted dolphins as well as other delphinids (Edwards 1992, 2006), theoretical models have been used to estimate cost of swimming at various speeds for spotted dolphins ranging in size from birth through adult, using morphological parameters based on measurements from spotted dolphins killed during tuna purse-seine operations in the ETP (Edwards 1992, 1993, 2002, 2006). These models were motivated by concerns about the effects of tuna purse-seine set evasion on spotted dolphins swim performance and energetics.

Although the direct energetic cost of swimming at speeds typical of tuna purse-seine set evasion for typical set durations plus aftermath (Chivers and Scott 2002) does not appear to add more than a few percentage points to the estimated daily cost of transport for mature spotted dolphins (e.g., an added 5-7% energy required due to

evasion of a single set, Edwards 2002), the consequences for calves appear to be much more severe, particularly for the younger animals which under normal circumstances draft close to their mothers but are likely to become separated and have to swim independently during tuna purse-seine set evasion (Noren and Edwards 2007). The smaller size and therefore smaller amount of power-producing muscle in calves, and the exponential (to the power of 3) increase in energy cost to swim as velocity increases, leads to great discrepancies between the power requirements of calves and adults swimming the same speed (Edwards 2006).

Estimated swim speed durations and costs for spotted dolphins ranging in size from birth through adult indicate that mass-specific cost of independent (non-drafting) swimming for the neonate is 3.6 times the cost for an adult swimming the same speed (Edwards 2006). Even in two-year-old spotteddolphins, estimated cost of swimming at any speed remains 40% higher than the cost for adults swimming the same speed. Estimated velocity durations for adult spotted dolphins range from burst speed (sustainable for a few seconds) of about 6 m sec^{-1} (208 W kgm^{-1}), through maximum speed (sustainable for a few moments) of about 4 m sec^{-1} (67 W kgm^{-1}), to prolonged (cruising) speeds of about 1-2 m sec^{-1} (4-10 W kgm^{-1}). Estimated swim speeds for neonates producing similar power outputs range from about 3 m sec^{-1} while producing 200 W kgm^{-1}, about 2 m sec^{-1} while producing 70 W kgm^{-1}, and less than 1 m sec^{-1} while producing 5-10 W kgm^{-1} (Edwards 2006). Actual *in situ* differences between speeds achievable for specific power outputs are likely greater because these model estimates don't account for positive buoyancy, reduced aerobic capacity, floppy fins and flukes, smaller proportion of muscle, and physiologically undeveloped muscle characteristic of neonate delphinids (Noren and Edwards 2007). These results imply that the common observation of drafting by dolphin calves through at least the first few months of life (including spotted dolphins in the ETP, based on aerial photographs) (Weihs 2004) is required for calves to maintain proximity to their mothers, as calves will lack the physical capacity to maintain that association while swimming independently (Noren and Edwards 2007).

Empirical measurements of burst (maximum achievable) swim performance by a trained spotted dolphin (subadult male) swimming independently along a straight 25 m course is the fastest recorded (Edwards 2006) for any delphinid under experimental conditions (11.02 m sec^{-1}) (Lang and Pryor 1966) but was sustained for only about 1.5 seconds, decreasing 10-20% soon thereafter. Maximum power output during the three fastest runs by this animal were 387, 419, and 461 kg m s^{-1}, compared to maximum human power output of 475 kg m sec^{-1} during one movement of arms and legs. Speed trials with two other spotted dolphins swimming a 70 m circular path resulted in maximum speeds of 7.7 – 8.3 m s^{-1}, 2-3 seconds after starting to swim (Lang and Pryor 1966).

Wild spotted dolphins rarely if ever produce this level of power output (Edwards 2006). Swim speed under natural undisturbed conditions tends to average 1-2 m s^{-1} (Leatherwood and Lungblad 1979, Perrin et al. 1979, Chivers and Scott 2002). During

evasion of tuna purse-seine sets, spotted dolphins have been observed to increase swim speeds, to 1.7-2.8 m s^{-1} during chase prior to set and 2.6-3.1 m s^{-1} after release, sustaining these higher exit speeds for up to 90 minutes (Chivers and Scott 2002).

It is not known whether swim performance in spotted dolphins is affected by blood oxygen content or heart weight, but it is possible, as other delphinids have exhibited oxygen capacities and heart weights related to swim performance (Ridgway and Johnson 1966). For example, the blood oxygen content of the extremely fast-swimming Dall's porpoise (*Phocoenoides dalli*) is 1.7 times that of the larger and less fleet *Lagenorhyncus obliquidens*, and 3 times that of the (even) larger and relatively sluggish bottlenose dolphin, *Tursiops truncatus.* Heart weights follow a similar trend, being greatest in *Phocoenoides dalli,* intermediate in *Lagenorhyncus obliquidens*, and smallest in *Tursiops truncatus.* Heart weight in spotted dolphins appears to be smaller that in any of the three species described above, perhaps implying a lesser capacity for swim performance (Ridgway and Kohin 1995).

THERMODYNAMICS (Heat Flux)

Blubber thermal properties, composition, and thickness in spotted dolphins (about 1.0 cm) (Boice et al. 1964, Worthy and Edwards 1990, Edwards 1993) reflect this species' tropical habitat. Blubber conductivity is significantly higher, lipid content significantly lower, and mid-lateral blubber depth significantly thinner in tropical-dwelling spotted dolphins, compared to *Phocoena phocoena* inhabiting cold-temperate habitats (0.2 vs. 0.1 W m^{-1} 0C^{-1}, 55% vs. 82%, and 0.8 cm vs. 1.5 cm, respectively, Worthy and Edwards 1990). In addition, surface area of spotted dolphins is greater than that of a *Phocoena phocoena* of similar mass. Although the seawater surrounding spotted dolphins in its tropical habitat is much warmer than the water surrounding dolphins in more temperate climates, it is still cooler than the delphinid core body temperature of about 37C (Hampton and Whittow 1976) so heat conservation remains an issue. As in the closely related *Stenella longirostris*, spotted dolphins appear to live close to their lower critical temperature, and may utilize activity, solar radiation, and control of blood (heat) flow to extremities to prevent hypothermia (Hampton and Whittow 1976). Accordingly, despite quantitative differences in characteristics related to heat flux, both spotted dolphins and *Phocoena phocoena* apparently use a combination of surface area, insulative quantity and insulative quality to thermoregulate effectively in their respective environments.

In the ETP, heat dissipation as well as heat conservation may be an important issue for spotted dolphins responding to sets by tuna purse-seiners. Because tuna-set evasion tends to involve sustained periods of relatively high-speed swimming both before capture and following release (Chivers and Scott 2002), these periods of prolonged, high intensity exercise will produce significant amounts of muscle-generated heat. This heat must be dissipated to avoid overheating of dolphin internal structures, including testes in males and developing fetuses in the uterus of pregnant females. Under most circumstances, dolphin overheating due to exercise is prevented by vascular countercurrent heat exchangers which utilize cooled blood coming from superficial veins

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in the blubber, flukes, and especially the dorsal fin to remove heat from nearby arteries (McGinnis et al. 1972, Hampton and Whittow 1976, Meagher et al. 2002). For example, studies of bottlenose dolphins indicate that both the uterus and testes in delphinids are associated with countercurrent heat exchangers that function to cool these reproductive organs (Rommel et al. 1992, Rommel et al. 1993), with exercise leading to increased cooling due to increased blood flow rates through the various structures (Pabst et al. 1995). Under natural circumstances, free swimming appears to readily remove excess heat to the environment (Pabst et al. 2002).

However, extensive, sustained exercise can result in heat accumulation. While short-term evasive swimming in response to chase by tuna purse-seiners did not result in elevated skin temperatures once swim-speed returned to normal, chase times greater than 75 minutes did result in elevated skin temperatures, suggesting sustained high rates of heat delivery to the skin's surface (Pabst et al. 2002). These measurements were taken from adult dolphins. Dolphin calves are likely to experience heat stress sooner than adults, after shorter periods of high-speed swimming, due to their smaller musculature and much higher power demands for swimming at adult speeds (Edwards 2006).

Blubber characteristics may also contribute to potentially greater heat stress in calves and pregnant females compared to non-pregnant adults. Studies of blubber thermal properties in bottlenose dolphin adults and developing calves found that blubber conductivity was lowest, and thermal insulation values highest, in calves and pregnant females (Dunkin et al. 2005). If the same patterns apply to spotted dolphins, then calves and pregnant females may be more likely than non-pregnant adults to experience heat stress at lower swim speeds as well as increased sensitivity to high water temperatures.

It is also possible that spotted dolphins may be more sensitive to heat stress than the more commonly studied bottlenose dolphins (*Tursiops truncatus*), because their thin blubber layer will not provide the heat sink apparently available to those dolphins with thicker blubber. Increased heat flux at deep versus superficial blubber sites (Dunkin et al. 2005) and cool rectal temperatures despite water temperatures elevated above skin temperatures (Heath and Ridgway 1999) in bottlenose dolphins, indicate that blubber can absorb heat from the deep body core. While spotted dolphins are more likely than bottlenose dolphins to experience ambient water temperatures approaching their core temperature, they do not appear to be equipped to utilize their (thin) blubber layer as a temporary heat storage facility. The ready availability of cool water below the thermocline in pelagic environments may eliminate any need for such heat storage, but it might conceivably be a problem for spotted dolphins in warm, shallow nearshore environments.

DEVELOPMENT

Developmental changes occur in various body components of spotted dolphins throughout the animal's lifespan, but the most dramatic tend to occur prenatally. More gradual changes occur during the perinatal period and during the first two or three years postpartum. Relatively few developmental changes occur after maturation.

Prenatal Development

Embryonic developmental stages 1-6 (sensu Štěrba et al. 2000; stages C9-C19 in Thewissen and Heyning 2007) in spotted dolphins, during which organ systems are established, occur during growth from about 21 mm to about 75 mm total length (0.6-2.2 g). *Fetal* developmental stages 7-11 (fetal stages F20-F23 in Thewissen and Heyning 2007) commence after organ development is completed and continue to a final fetal size of about 945 mm total length (Štěrba et al. 1994, 2000, Thewissen and Heyning 2007). Total body weight gain accelerates and flukes and flippers begin developing during the first fetal stage (Stage 7). Not all body dimensions change size smoothly; for example, total length increases faster during some stages than others (Štěrba et al. 2000). Very early embryos of spotted dolphins tend to be similar to very early embryos of terrestrial mammals at a similar developmental age (e.g, an olfactory bulb is present), but cetacean-specific structures soon begin to develop, including the characteristic uncoupled ear complex, a beak-like larynx, flippers, fins, a shortened and fused neck, and the cetacean body shape (Rauschmann et al. 2006). In addition, the olfactory apparatus begins to develop, but then regresses and disappears. Prenatal development of cetacean characteristics in spotted dolphins has been studied in detail in several skeletal as well as soft tissue systems, including head pigmentation, integument, ears, skeletal elements (skull, teeth, neck vertebrae, limbs) and organs (heart, lungs, and terminalis system), as summarized below.

Head Pigmentation. The "bridle stripe system" of head striping in adult spotted dolphins, consisting of the eye stripe (stripe extending forward from the eye), the blowhole stripe (stripe extending forward from the blowhole), and the gape mark (dark mark that edges the gape), first appears as a distinct dark band far behind the blowhole across the neck in fetal spotted dolphins approximately 82 mm in length (Perrin 1997). By 136 mm fetal length, the eye stripe and blowhole stripe are clearly visible. At 198 mm, the eye stripe is completely defined, the blowhole stripe is still a "cap", and bridle coloring differs only slightly from the patterns seen in *Stenella longirostris* and *Delphinus delphis*. At 218 mm, the eye spot has changed from light gray to dark grey and the posterior margin of the "cap" has reached its anterior-most position, nearly in contact with the ends of the blowhole slit. At 243 mm, the very light-grey circles bordering the eye and blowhole in spotted dolphins are very bright, but by about 330 mm, the bright zones have almost disappeared, the eye spot is bordered by a darker-grey zone, and the blowhole stripe is now recognizable. Unlike *Stenella longirostris* and *Delphinus delphis*, the eye stripe in spotted dolphins does not meander onto the rostrum and return to join the blowhole stripe near the apex of the melon. At 335 mm, the eye stripe in spotted dolphins has reached its final configuration, although the blowhole stripe has not. In postnatal spotted dolphins, the eye stripe varies in width, may be composed of a single simple stripe or a dark stripe embedded in a broader, lighter-gray band, and does not appear on the rostrum. The blowhole stripe varies little, consisting usually of a dark band the width of the blowhole, demarcated by narrow light lines. The bridle in spotted

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dolphins appears to be roughly typical of that found in the delphinoid families Delphinidae and Phocoenidae, as opposed to the family Monodontidae which does not appear to develop a bridle pattern, suggesting a closer relationship between the former two taxa (Perrin 1997).

Integument. The integument of spotted dolphins is the animal's largest organ system and includes the epidermal, dermal and hypodermal layers of the encompassing blubber coat. During prenatal development of the integument in spotted dolphin embryos, the *stratum basale* produces four different epidermal generations, concluding with production of the *stratum spinosum* at about 225-260 mm body length (Meyer et al. 1995). The dermis begins to appear as thin connective tissue fibers at about 40-70 mm, as the cutaneous muscle matures in structure. The hypodermis develops rapidly and constantly from about 60 mm body length and the first typical fat cells appear at about 380 mm body length. Vascular development intensifies at about 200 mm body length, collagen production increases markedly thereafter, and dermal thickness increases concommitantly. The epidermis continues to thicken throughout the remainder of the prenatal period, with epidermal ridge formation beginning at about 400 mm body length. The first elastic fibers can be recognized in the abdominal skin at about 600 mm body length. Structural maturation is more rapid in the flippers than in dorsal or abdominal regions (Meyer et al. 1995).

Ears. Prenatal ear development in spotted dolphins, as is common among mammals, begins with the inner ear structures first, followed by peripheral structures of the outer and middle ear (Solntseva 1990). As in other mammals, the period during which the peripheral auditory system develops in prenatal spotted dolphins extends from formation of the auditory vesicle to completion of the main structures of the system, during formation of the cartilaginous skeleton. By the end of early embryogenesis of the peripheral auditory system the cochlea is greatly enlarged compared to the vestibular apparatus (almost 2-fold), and the main formation process in the outer ear is completed (Solntseva 1999).

Meatus. The external auditory meatus is formed before birth in cetaceans. The ear canal (auditory meatus) in odontocetes, including spotted dolphins, is initially formed when the fetus is about 30-40 mm long (Solentseva 1990). The meatus is a short tube initially, which later distends, bends, and acquires an s-shaped form, growing thereafter in absolute dimensions in proportion to growth of the embryo (Solentseva 1999). The meatus becomes constricted by embryo size 40-60 mm, and the S-shape expands in the proximal section but remains constricted in the distal section when the fetus is about 70-100 mm long (Solentseva 1990). The tympanic membrane-ligament develops during embryo to fetal growth from about 40 mm to about 100 mm total length (Solentseva 1999). The tympanic bulla becomes separated from the cranium, and the S-shaped auditory meatus becomes completely filled with epithelial cells. Before birth the epithelial cells in the proximal portion of the meatus are resorbed, although part of this embryonic plug persists and later serves as a basis for formation of the epithelial tissue of an adult canal (Solntseva 1999).

Middle Ear. The middle ear is formed as a tube-like protrusion of the first pharyngeal pouch, comprising a narrow blind canal running under the rudimentary ossicles, the contours of which can be clearly seen as separate components (Solentseva 1999). Cetacean middle ears, including those of spotted dolphins, are unique among mammals in having an elongated tympanic membrane, a greatly reduced *manubrium mallei*, and an *incudal crus longum* that is shorter than the *crus breve* (Kinoshita et al. 2001). Mesenchymal, cartilaginous, and osseous development of cetacean middle ear structures indicate that some of these unique structures develop as substantial modifications of an initially terrestrial-like morphology, so that the morphology of the adult cetacean ear is quite different from that found in early prenatal cetaceans (Kinkel et al. 2001).

In spotted dolphins, as in other odontocetes, anlages of the middle ear ossicles (malleus, incus, and stapes) are already separate from the anlage of the tympanic cavity in embryos 20-30 mm long (Solentseva 1990). Ossicle articulations appear, the tympanic cavity begins to form, and ossicles begin to insert into the posterior tympanic space by 30-40 mm length. In embryos 50-60 mm long, the incus and malleus are located at right angles to each other, the stapes form a column, and cavernous tissue is observable in the middle ear cavity. Middle ear muscles appear in embryos 40-80 mm long and are completed in fetuses 90-100 mm long. Specific peribullar sinuses that separate the tympanic bulla from the skull are not present during early embrogenesis but are formed in fetuses 200-250 mm long. The ossicles are cartilaginous in embryos up to 70-80 mm in length, with cartilage replaced by osseous tissues in 90-100 mm fetuses. These bony ossicles are not as dense as in adults. During early development, all three ossicles are slender as in primitive, adult terrestrial animals, but they become much larger and less flexible during later development (Solentseva 1990). In addition to increasing density, the entire incudomallear complex reorients by about 90 degrees during development, bringing the incudomallear joint and includal crura into their adult positions; this rotation is followed by elongation of the tympanic membrane (Kinoshita et al. 2001, Moran et al. 2011).

By the end of early embryogenesis of the peripheral auditory system in the middle ear of the Odontoceti, the cavernous plexus is formed and the venous sinuses appear in the osseous part of the auditory meatus (ear canal), with the peribullar sinuses found between the cranial wall and the cochlear capsule (Solentzeva 1990). Pressure changes in the middle ear of toothed whales during diving are regulated by these cavernous tissues, which are unique to aquatic mammals (Solentseva 1999).

Inner Ear. Development of the inner ear in spotted dolphins is similar to that in other odontocetes (Solntseva 1983, 1990, Klima 1995, Solntseva 1996, Klima 1999, Solntseva 1999, 2002). The inner ear appears much earlier than the middle or outer ear during embryogenesis, forming from thickened ectoderm which originates from the anlage of the labyrinth membraneous (Solentseva 1990). The auditory vesicle splits into an upper part, which becomes the vestibular apparatus, and a lower part, which becomes

the cochlear canal. The cochlear canal then begins twisting into a spiral shape to form the basal turn of the cochlea. The inner ear is already differentiated into initial cochleate and vestibular structures in embryos 20-30 mm long, with the cochleate structure being much larger than the vestibular structure (in contrast to pinnipeds and humans). The middle turn of the cochlea is formed in the inner ear at the same time as the middle ear cavity enlarges. Differentiation of the cochlea into basal and apical turns, and widening of the basal turn, is observable in embryos 30-40 mm long. Vestibular structures form in embryos about 40-60 mm long, the cochleate and vestibular branch is visible in embryos 60-80 mm long, and the secondary osseus spiral lamina in the cochleate canal, the basal membrane, and the completed cellular differentiation of the organ of Corti are visible in fetuses 100-150 mm long. Although the structure of the cochlea in the inner ear is similar in almost all mammals, the number of turns is species-specific. In spotted dolphins, two turns are found in the cochlea upon completion of the cochlear apical turn (Solentseva 1999).

Skull. Prenatal development of the nasal skull in spotted dolphins is similar to development in other odontocetes (Solntseva 1983, 1990, Klima 1995, 1999, Solntseva 1999, Armfield et al. 2011, Moran et al. 2011) and is distinct from that of terrestrial mammals in the very earliest anlage (Klima 1995). Nasal skull morphology of embryos up to about 40 mm in length tends to be similar in all cetaceans, including spotted dolphins. As embryos grow larger, differences between groups begin to develop, so that by the time embryos reach about 90 mm total length, specimens can be identified as baleen whales, sperm whales, and other toothed whales (including spotted dolphins) (Klima 1995). While spotted dolphin embryos less than about 25 mm total length possess almost no nasal structures, the morphogenetic process is nearly completed by about 150 mm total length (Klima 1999). Subsequent development through about 225 mm total length includes intensive tissue vascularization and ossification of dermal bones (Klima 1999). Components of a cartilaginous nasal capsule including an olfactory bulb and tract become clearly visible during early prenatal development (Rauschmann et al. 2006). At this time, accessory air sinuses are absent and most nasal area structures are still very immature, with each nasal tube having only two small bud-like projections. Morphogenesis of the embryonic cartilaginous nasal skull leads to displacement of the nasal openings from the rostral tip to the parietal pole of the head. Olfactory structures and function are lost, simplifying the whole nasal capsule which rotates from a horizontal to a vertical position (Rauschmann et al. 2006). "Simultaneously, the septum nasi elongates and projects into the cartilaginous nasal rostrum. This and related cartilaginous structures form a basis for dermal bones, especially the maxillae and premaxillae, which develop later. All the structures participate in building the typical protruding cetacean rostrum, combined from the cartilaginous structures as the dermal bones" (Klima 1995).

Teeth. Tooth development in the homodont embryo of spotted dolphins is similar in early stages to development in the terrestrial heterodonts (e.g., domestic sheep and field vole) with all embryos exhibiting a lateral enamel lamina (LEL) (Witter et al. 2002). The LEL appears during tooth development of all mammals, although its function is unknown. It is part of the enamel organ during development but is probably not involved in tooth

formation and undergoes regression during morphogenesis of the enamel organ. The LEL is most clearly observable in slowly developing tooth germs as part of the enamel organ during the cap to bell stages. However, although the LEL can be detected in the cap-stage tooth germs of spotted dolphins, reduction begins at an earlier developmental stage than in other species examined. In spotted dolphins, only the proximal part of the lamina apparatus remains detectable in the cap and bell stages, while the distal part near the oral epithelium is reduced (Witter et al. 2002).

Neck Vertebrae. In adult spotted dolphins, as in many other cetaceans, the rostral-most cervical vertebrae (C1 and C2) fuse to form a single heavy bone, with C1 dominating in size (Kappesser and Oelschläger 1999). The other cervical vertebrae tend to be highly compressed with thin intervertebral disks. This shortening and modification of the cervical vertebral column in cetaceans leads to limited cranial movement laterally and dorsoventrally and allows no rotation about the axis. These modifications likely contribute to stability of the head relative to the rest of the body during swimming, contributing to increased hydrodynamic efficiency. These cervical changes begin very early during prenatal development. During embryonic development in spotted dolphins, each cervical vertebra arises as a separate skeletal element. During early fetal development, the cervical vertebral column (CVC) consists of a strong rostral complex (C1 and C2) and a homogeneous series of wide but very thin vertebrae (C3-C7). The notochord runs through the center of the cervical vertebrae, although bone formation has not yet begun at this stage. The atlas (C1) and axis (C2) comprise two-fifths of total CVC length, and are both thicker and wider than the following vertebrae (C3-C7). During fetal development, C7 adjusts to fit the proportions of the first thoracic vertebrae, but vertebral fusion is not yet complete (Kappesseer and Oelschlaeger 1999).

Shoulder Girdle. Shoulder development in spotted dolphins, as in other ceteceans, differs considerably from that of terrestrial mammals. A clavicle appears temporarily during embryogenesis, with the first anlage of the clavicle appearing when the embryo is about 39 mm and persisting at least through a fetal size of about 85 mm (Klima 1990). Clavicle development occurs in the same general topographical position as in animals possessing a full shoulder girdle, between the sternum and the acromion, but the clavicle is too small to bridge that distance. The clavicle stems histogenetically from dermal ossification, independent of the special histogenetic mode of osteogenesis. Ossification proceeds briefly, but the bone processes soon become opened and decomposition processes take over during subsequent development. The clavicle is subsequently dissolved by osteoclasts and finally the anlage decomposes completely (Klima 1990).

Limbs. In spotted dolphins, well-developed hind limb buds as well as conical forelimb buds are visible at 24 days, but by day 48, the hindlimb buds are largely regressed; in contrast, the forelimbs continue to grow so that by day 48, well-developed digital primordia can be seen (Bejder and Hall 2002, Thewissen et al. 2006).

   Forelimbs. With regard to locomotion, forelimbs of Cetacea, including spotted dolphins, tend to serve as stabilizers rather than contributing to propulsive movement.

The presence of numerous stiff-jointed phalanges joined together beneath a smooth epidemis creates a firm and strong but also elastic structure with good hydrodynamic properties, very similar in function to a fish's fin (Sedmera et al. 1997b). The only moveable articulation in the entire limb is the shoulder joint. The humerus and forearm are markedly shortened and the "finger joints" are stiff. While each flipper encases the "usual" 5 digits, these digits, particularly those in the middle, include more individual bones than found in a terrestrial mammal's "hand" (Sedmera et al. 1997b). Also in contrast to terrestrial mammals, in which the number of phalanges is usually constant, the phalangeal formula in Cetacea differs considerably not only among individuals, but also during the total life span, with the number of phalanges peaking in late fetal life rather than during adulthood (Sedmera et al. 1997b, Bejder and Hall 2002).

In spotted dolphins, the forelimb (flipper) buds are very similar to those in other mammals at the earliest stages of development, but considerable differentiation is soon apparent and chondrogenesis begins to proceed proximodistally (Sedmera et al. 1997b). The shape of the developing limb then changes, with a relative increase in the length and width of the digital plate but slower growth of the proximal structures. Differentiation continues with a gradual change in the original oval shape of cartilaginous elements to adult polygonal form. Hyperphalangy develops as the number of digital elements in each "finger" increases from 2,3,3,3,0 at about day 40 to 3,7,7,5,3 at about day 87 (Sedmera et al. 1997b). The greatest proliferation occurs on digits II and III (Richardson and Oelschläger 2002). Proximo-distal development of phalanges is prolonged in these digits, with longer persistence of the cap or ridge forming part of a bud-like mass. The forelimb of spotted dolphins thus differs from that of terrestrial mammals by having a second period of limb outgrowth during which localized hyperphalangy develops, with new phalanges forming only at the tip of the digits, rather than within the digit as a result of secondary splitting of primary phalangeal digits. This prolonged period of limb outgrowth is the likely mechanisim underlying hyperphalangy in spotted dolphins (Richardson and Oelschlager 2002). Ossification of the phalanges begins in the girdle region and progresses distally from there. Joint development is arrested so that joints remain in a primitive state, joined together by dense connective tissue rather than forming synovial spaces (Sedmera et al. 1997b). Postnatal growth of the forelimb in spotted dolphins is rapid, with the individual bones increasing to near adult shape within the first three years, after which growth rate slows while physical maturity is reached (Perrin 1975a). In general, ossification is minimal at birth and increases, along with phalangeal number, as the animal matures (Perrin 1975a).

Hindlimbs. Hind limb loss during prenatal development in spotted dolphins results from arrested development at the limb bud stage, due to an inability to maintain necessary inductive tissue interactions, as well as from enhanced cell death (Sedmera et al. 1997a, Bejder and Hall 2002). The external shape of the hind limb buds in early spotted dolphin embryos (about 21-70 mm total length) is quite similar to that observed in other vertebrate embryos (Sedmera et al. 1997a). Some histodifferentiation occurs, with formation of mesodermal condensations or sometimes early primitive precartilaginous rudiments (Sedmera et al. 1997a). However, "examination of gene

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expression during early development of hind limb buds in spotted dolphin embryos indicates that the molecular cascade that controls limb development deviates from that described for other tetrapods" (Thewissen et al. 2006). Although the hindlimbs point caudally, they are considerably smaller than the forelimb buds and become relatively shorter and more cone-like over time (Sedmera et al. 1997a). Two signaling centers of growth are found normally in developing mammalian embryos; the AER (apical ectodermal ridge) and the ZPA (zone of polarizing activity) (Thewissen et al. 2006). Spotted dolphin embryos develop only an AER, which soon undergoes regression. The gene responsible for AER production operates only briefly, and the precursor gene (Hand2) to that which controls ZPA production (Shh) is missing altogether so that ZPA is never initiated. Subsequently, the AER gradually regresses, the ectoderm thickens laterally, and signs of degeneration can be detected in the mesoderm (Thewissen et al. 2006). The limb buds gradually regress during subsequent stages, until the last recognizable hind limb rudiment is transformed almost completely into a skin fold that later disappears (Sedmera et al. 1997a), so that pelvic limb buds have disappeared by the end of Stage 6 (C18-C19 in Thewissen and Heyning 2007). The disappearance of hind limbs in spotted dolphins, as in other cetaceans, is an evolutionary adaptation in which caudal fluke stroking replaces hind limb ambulation (Sedmera et al. 1997a). It appears that the initial reduction in hind-limb size of spotted dolphins resulted from gradually-operating microevolutionary processes, rather than from macro-evolutionary changes in gene expression (Thewissen et al. 2006).

Heart. During embryological development of spotted dolphins, the heart completes septation at about 35 days, while trabecular compaction and coronary circulation is complete at about 60 days (later than in some other mammals) (Sedmera et al. 2003). The heart gains a compacted, characteristic shape with a single apex (unlike the bifed apex found in adult sperm whales and sireniens) at about day 80. The delay in timing of heart compaction is similar to delays observed in ossification and odontogenesis (Štěrba et al. 2000, Sedmera et al. 2003).

Lungs. Lungs of spotted dolphins remain in a glandular stage of development until about 3 months post-implantation (pi), achieve cannicular stage by about 3.5 months pi, and develop mesenchymal rings and muscular bands in a sphincter-like arrangement around terminal bronchioles by about 4 months pi (Drabek and Kooyman 1983). The alveolar stage is apparent at 7 months pi, and cartilaginous rings are associated with myoelastic sphincters by about 8-9 months pi (Draybeck and Kooyman 1983).

The glandular stage involves "an extensive network of endodermal tubes with a simple columnar epithelium lining the lumina. The smallest measurable tube is 20-30 µm in diameter. Scattered smooth muscle cells are seen around the walls of a tube having a diameter greater than 75 µm" (Drabek and Kooyman 1983). During the cannicular stage of development, the glandular appearance of the lung is replaced by well-formed, semilunar mesenchymal blocks arranged adjacent to poorly-developed smooth muscle bands along the airways. At about 3.3 months pi, cartilage begins to support the walls of the larger bronchioles (approximately 375 µm) and the spaces of

incipient alveolar sacs are much more uniformly distributed. By the alveolar stage, multi-lobed alveolar sacs occur throughout the specimen matrix. Smooth muscle is arranged as sphincters at the entrance to the alveolar sacs, which have an average length of 148 µm (range: 25-400 µm) and average width of 11 µm (range: 0-60 µm). Cartilage appears in the terminal airways at 8.4 months pi, by which time the supported sphincter muscles are well developed. By 9.5 months pi, the entire matrix is composed of alveoli making up alveolar sacs, and alveolar sac dimensions have increased to an average length of 271 µm (range: 110-500 µm) and average width at sac entrance of 42 µm (range: 10-105µm). Cartilaginous blocks associated with each myelastic sphincter appear as components of the cartilaginous rings that support the terminal airways. The average number of blocks per sphincter is 2.9 in near-term fetuses and 2.3 in neonatal spotted dolphins. The average dimensions of alveolar sacs is larger in neonates than in fetuses (381µm (120-780 µm) average length, 63 µm (10-185 µm) average width at entrance), and in the four oldest neonates examined, cartilage and sphincter muscles ringed the terminal airways (Drabek and Kooyman 1983).

The airway structure of neonate spotted dolphins indicates the ability to achieve a low minimum air volume (MAV) similar to that found in other marine mammals with cartilaginous support to the alveolar sac (Drabek and Kooyman 1983). The degree of cartilaginous reinforcement in the spotted dolphin neonate would also enable it to maintain high expiratory flow rates despite low lung volume. The myoelastic sphincters in terminal bronchioles probably function to prevent alveolar collapse during the ambient hydrostatic pressure increase associated with diving. The presence of well-developed sphincters and cartilage in the neonate indicates that the as-yet-undetermined function(s) of these structures, which are peculiar to some cetaceans, pertain at birth as well as in adulthood (Drabek and Kooyman 1983).

Terminalis System. Odontocetes, including spotted dolphins, differ substantially from terrestrial mammals in prenatal development of the placode responsible for development of the closely associated olfactory, vomernasalis, and terminalis systems (Buhl and Oelschläger 1986, Oelschläger et al. 1987). In terrestrial mammals, terminalis neuroblasts reduce in number during the fetal and postnatal periods while the olfactory bulb and vomernasal organ continue to develop. During prenatal development in odontocetes, the placode morphs primarily into the terminalis system, with little development of the olfactory or vomernasalis systems. Although the odontocete anlage of the nasal cavity forms in the same manner as in other mammals, the near-by (in other mammals) vomeronasal groove and nerve never develop. Because the anosmatic dolphins and toothed whales never produce a vomeronasal organ and the olfactory system appears only briefly during embryogenesis, development of the terminalis system, which is often difficult to determine in in other mammals, can be clearly followed in odontocetes from the beginning of the fetal period. The well-developed odontocete terminalis possesses terminalis ganglia of remarkable size, "possibly containing the maximal number of neurons to be found among the Mammalia" (Oelschläger et al. 1987).

Examination of early development and fetal topography of the terminalis ganglion and nerve in the human as well as in five odontocete species (including 11 spotted dolphins ranging in size from 21 to 89 mm total length), revealed that even the smallest odontocete specimens showed no sign of vomero-nasalis system development, and development of the olfactory system ceased at the end of the embryonic period (Buhl and Oelschläger 1986, Oelschläger et al. 1987).   The terminalis ganglion in odontocetes develops distinct from the primordial olfactory nerve fiber trunk, and continues to develop into an isolated terminalis ganglion. The nervous terminalis ganglion of the brain of spotted dolphins embryos is relatively small during early development, compared with that of *P. phocoena,* but is already well separated from the olfactory bulb, with the terminalis ganglion being completely separate from the degenerating olfactory bulb in embryos of about 60 mm total length.   Although the olfactory bulb begins to develop, it subsequently disintegrates into its components, one of which contains the the material of the future terminalis ganglion, which is easily discernible by the large cell size and dark staining, similar to other developing cranial ganglia (Oelschläger et al.1987).

During fetal development in odontocetes (including spotted dolphins), some peripheral terminalis nerve fiber bundles enter the cranial cavity through several openings, while others remain as peripheral terminalis ganglia below the forming cribriform plate near the nasal mucosa (Oelschläger et al. 1987).   Within the skull, the terminalis rootlets extend toward central attachment sites, including lamina terminalis, olfactory tubule, ventral septal region, and brain wall. Overall, the ganglion connects with the nasal mucosa via peripheral nerve fibers and with the telencephalon via central terminalis rootlets. The central carotid artery has regressed in odontocetes, and there are no cervical sympathetic ganglia to enervate the intracranial arteries (Oelschläger et al. 1987).

The function of the terminalis system in the nasal region of the mammalian head is not fully understood in either terrestrial or aquatic mammals, although it appears to function at least in part, in maturation and differentiation of the brain-pituitary-gonadal axis (Oelschläger et al. 1987). In odontocetes, the terminalis system may contribute to gonado-trophic functions (based on close intermingling of terminalis and olfactory components in land-based mammals and the high number of terminalis neuroblasts and the enormous size of male gonads in the adult odontocete) and to regulation of blood flow and mucous secretions via the autonomic system (to facilitate emission of high-frequency sound signals). Based on the large size of the odontocete terminalis system, it may also contribute to regulation of blood flow through a *retia mirabilia* in the area of the brain during diving. Autonomous function is suggested to exist in both parasympathetic and sympathic terminalis components in odontocetes, the former for innervation of mucous glands in their acquired accessory nasal air sacs with extensive epithelial surface, and the latter for innervation of the plexuses (*rete mirabilia*) along the anterior cerebral artery. The terminalis system in odontocetes does not appear to include a sensory (e.g., smell) function (Oelschläger et al. 1987).

Perinatal Development

<u>Skull.</u> Skull morphology of perinatal spotted dolphins is generally similar to adult skull morphology with the exception of a much shorter rostrum and incomplete development of a few related structures (Rauschman et al. 2006). The cranial vault and brain are wider than long. While the symmetrical nasal complex of early fetuses has begun to transform asymmetrically, the midsagittal plane of the nasal area in perinatal spotted dolphins is shifted only slightly to the left, much less so than in adults. The telescoping process is not yet completed, so "the caudal extensions of the maxillary bones do not yet meet the dorsorostral margin of the supra occipital and there is no trace of the transverse supraoccipital crest of adult spotted dolphins" (Rauschman et al. 2006).   Remaining rostral development is associated with one of the few examples of incomplete development of the skull in perinatal spotted dolphins*:* wide gaps between the lateral skull and the presphenoid, orbitospenoid, and mesethmoid, which close sometime prior to adulthood (Perrin 1975b). Adult status in spotted dolphin skull morphology is defined by fusion of the premaxillaries and maxillaries at the distal end of the rostrum (Perrin 1975b).

The lower jaw of perinatal spotted dolphins fits perfectly to the temporomandibular joint, including meshing of upper and lower teeth (Rauschmann et al. 2006). As in adults, the lateral wall of the dentary is very thin, likely contributing to sound reception via the mandibular fat body and tympanoperiotic complex. Perinatal spotted dolphins do possess a "secondary zygomatic arch" similar to that found in adults, with a dense connective tissue bridge separating the blunt processes of the frontal and squamosal bones. The connective tissue likely guarantees mechanical stability as well as preventing bone conduction of sound. Not surprisingly in an animal that does not chew its food before swallowing, the masticatory apparatus of perinatal (and adult) spotted dolphins is relatively reduced and simplified compared to those of carnivorous terrestrial mammals, and there is no evidence of salivary glands, including the parotid gland (Rauschmann et al. 2006).

<u>Brain.</u> Adult brain morphology appears to be present in perinatal spotted dolphins (Rauschman et al. 2006). The brain of perinatal spotted dolphins is large and highly differentiated, with a well-developed brainstem, a large thalamus and hypertrophied auditory system, as well as a large metencephalon (cerebellum and pons), and myelencephalon (brain stem and fiber tracts for auditory and trigeminal systems) (Rauschman et al. 2006).

<u>Eyes.</u> The visual system in perinatal spotted dolphins includes a thick optic nerve, with all nerves for external eye muscles present, and a spherical lens within an ellipsoid eyeball, likely contributing to nearsightedness (myopia) in the frontal (rostral) direction and normal vision in lateral (sideways, or axial) directions (Rauschmann et al. 2006).

<u>Ears</u>. Most ear structures in spotted dolphins appear to have developed sufficient maturity to function normally in postnatal dolphins, although some accessory structures do not complete development until about 10 days postpartum (Solentseva 1990). Similar

to adults, the ear of perinatal spotted dolphins includes a very narrow (nearly obliterated) soft external auditory meatus, ending in a pinhole-like external opening in the skin (Rauschmann et al. 2006). The tympanoperiotic complex, which houses the middle and inner ear components and includes the tympanic bulla and the periotic bones, is already present in early fetuses. In perinatal spotted dolphins, the tympanic bone has attained its characteristic bullar shape and the periotic is largely isolated from the skull by neighboring soft and dense connective tissue. These tissues and the very high-density tympanoperiotic structures, as seen in adults, presumably isolate the ears from the sound-generating structures of the skull area and provide a large "reference mass" for independent oscillation of the auditory ossicles in response to incoming sound. The middle ear is generally similar to adult structures, although the internal carotid artery is about 1 mm in diameter and still open, a condition not seen in adults. The cochlear nerve is as thick as the optic nerve. As in adults, the semicircular canals of the vestibular system in perinatal spotted dolphins are substantially reduced, being much smaller than would be expected (in other mammals) given the size of the cochlea and the size reached by adults. This reduced size may function to reduce vertigo or may have resulted from the shortened cervical region and limited mobility of the head, in cetaceans (Rauschmann et al. 2006).

Acoustic fat bodies (dorsal bursae, melon, and mandibular fat bodies) which consisted of loose connective tissue in early fetuses of spotted dolphins are fully differentiated in perinatal spotted dolphins (Rauschmann et al. 2006). The melon is well developed, with heterogeneous structure. The mandibular fat body and melon develop late in fetal development, in parallel with blubber fat. The lower jaw contains a long and slender mandibular fat body with characteristics similar to the melon tissue. In the caudal part of the mandible, where the fat body attains its maximal thickness, the lateral wall of the shell-like dentary bone is extremely thin but dense. The mediocaudal bony wall of the mandible has been totally reduced and its fat body extends so far caudally that it contacts the lateral lip of the tympanic bulla. The mandibular fat body is separated from the tympanic bulla only by the two adjacent periosts. In their area of contact, the two periosts (mandible, bulla) are rather thick and seem to be 'fused' with each other.

The acoustic system differs from that of adults in at least two ways: 1) the eighth cranial nerve is smaller in diameter than the trigeminal nerve (the reverse is true in adult spotted dolphins, and 2) a second channel of fatty tissue cannot be distinguished lateral to the tympanoperiotic complex in the perinatal spotted dolphin (Rauschmann et al. 2006). These morphological differences may imply differences in acoustic sensitivity between perinatal and mature spotted dolphins.

Nasal Complex. The nasal structure of perinatal spotted dolphins is similar to that of adults in size and shape, with only the mesorostral cartilage remaining of the original nasal capsule (Rauschmann et al. 2006). In contrast, the terminal nerve, originally co-located with the olfactory bulb, is retained and attains its maximal development within the Mammalia. The nostrils are fused at the blowhole into a single, rostrocaudally flattened vestibulum, and the internal nasal openings are perpendicular to the base of the

skull. The vestibulum opens ventrally into the paired soft nasal passages, with three pairs of nasal air sacs opening into the nasal passage.   These nasal structures generate and transmit sonar beams, creating sounds by vibrations in specialized small fat bodies (dorsal bursae) near the dorsal ends of the paired nasal tracts. These vibrations then move through and are focused by the melon. The ability to create these sounds is apparently near full development in perinetal spotted dolphins (Rauschmann, et al. 2006).

Larynx. The larynx in perinatal spotted dolphins is large and located ventral to the skull base, extending rostrally to form a goose-beak-like structure that prevents water from entering the airway between the posterior nasal apertures and the trachea (Rauschmann et al. 2006). The larynx also appears to be responsible for creating the air pressure needed for sound production (Cranford et al. 1996).

Postnatal Development

Total length of spotted dolphins at birth is ca. 85 cm (Perrin et al. 1976). Length at 1 year of age is about 129 cm in the ETP (Hohn and Hammond 1985) and about 142 cm in the western Pacific (Kasuya 1976, Kasuya et al. 1974), although this difference may reflect different analytical approaches (Perrin and Hohn 1994). Growth of males and females does not differ until a secondary growth spurt occurs in males at about the onset of sexual maturation (ca. 160 cm) (Perrin 2001).

External Color. Spotted dolphin coloring proceeds through five stages as the animal ages: newborn, two-tone, speckled, mottled, and fused. The color phases are only roughly correlated with specific ages (Archer and Chivers 2002) but in general, two-tone and speckled, and most mottled, are sexually immature, while almost all fused animals are mature (Perrin et al. 1976). The newborn calf is unspotted with dark dorsal and light ventral surfaces. Two-tones are also unspotted, with dark-grey and light-grey dorsal and ventral surfaces. Speckled animals are larger juveniles with distinct dark spots beginning to appear ventrally. Mottled animals are near-adult and sometimes young adult, with large discrete or overlapping spots both above (light) and below (dark). Fused animals are adults in which the ventral spots have fused and faded to a medium gray while the dorsal light spots have intensified, sometimes to the point of making the animal appear nearly white above. The light spots sweep up behind the dorsal fin. The underlying pattern (observable in calves and juveniles) consists of a dark cape sweeping over the eye to maximum depth below the dorsal fin, a very light to dark gray lateral/ventral field, a narrow well–defined eye stripe to the apex of the melon, a dark band of varying definition extending from the lower corner of the mouth to the flipper, and dorsoventral division of the peduncle into darker upper and lower lighter halves. The last can also be seen in adults. The tip of the beak is white in adults. Details of coloration vary regionally. For example, adults of the large coastal spotted dolphin in the ETP (*S. a. graffmani)* are extremely heavily spotted, whereas animals found farther offshore have much less distinct spotting (Perrin et al. 1976).

Internal Organs. Changes in body dimensions with age (and/or weight) have been studied in spotted dolphins from the ETP (Perrin and Roberts 1972, Perrin 1975b,

Edwards 1993) and the Pacific coast of Japan (Miyazaki et al. 1981). ETP specimens have been examined for postnatal growth in heart, lungs, liver, kidney, spleen (Perrin and Roberts 1972), skeletal components (Perrin 1975b), brain (Perrin et al. 1977; Figure 14 is *S. attenuata*, not *S. longirostris*), blubber, muscle, bone and viscera (Edwards 1993). Japanese specimens have been examined for both prenatal and postnatal growth in heart, lungs, liver, kidney, spleen, pancreas, first and second stomach, and intestine (Miyazaki et al. 1981). Comparisons between geographic areas can thus be made with respect to postnatal growth of heart, lungs, liver, kidney and spleen of spotted dolphins.

In spotted dolphins from the ETP, the percent of total body weight due to heart decreases with age (size), from about 0.73% in fetuses and infants, to about 0.48% in calves and immatures, finishing at about 0.43% in adults (Perrin and Roberts 1972). Computed relative heart mass in both spotted dolphins and *Stenella longirostris* is smaller than in three other dolphin genera (*Phocoenoides dalli*, *Lagenorhynchus acutus*, and *Tursiops truncatus*) (Ridgway and Konin 1995). Lungs average about 3.2% of adult body weight in spotted dolphins from the ETP, with a growth coefficient (GC) of 0.99, compared to a GC of 0.79 in spotted dolphins from Japan. Liver fraction of body weight in spotted dolphins from the ETP increases from about 1.8% in fetuses to about 2.5% in adults, with a gc of 0.92, compared to a gc of 0.73 in spotted dolphins from Japan. The differences between gcs of ETP versus Japanese spotted dolphins appear to indicate slower growth of some body parts in Japanese spotted dolphins, although these differences have not been investigated further.

Kidney fraction of total body weight changes inconsistently with age, from about 1.1% in fetuses to about 0.84% in calves and immatures, and to about 0.98% in adults; both Japanese and ETP spotted dolphins have a gc for kidney of about 0.98. The kidney o spotted dolphins from the ETP is 2-4% larger on the left than the right. Spleen fraction of total body weight also changes inconsistently with age in spotted dolphins from the ETP, decreasing from about 0.07% in fetuses to about 0.011-0.012% in calves and immatures, and ten increasing again to about 0.06% in adults, with a gc in males of 0.97 compared to a gc in females of 0.88. Growth coefficient of spleen in both sexes of spotted dolphins from Japan was about 0.57. Average absolute weight of the spleen follows a similar pattern, increasing from 4 gm perinatally to 31 gm in calves and 53 gm in subadults, and then decreasing to 31 gm in adults (Perrin and Roberts 1972). Growth coefficients in spotted dolphins from Japan (not reported for spotted dolphins from the ETP) were about 0.95 for pancreas, stomach, and intestine. Brain weight in spotted dolphins from the ETP increases from about 310 g in neonates (Ridgway 1986, Perrin 2001) to between 650-725 g in adults (Ridgway 1986, Perrin and Hohn 1994). This is somewhat smaller than brain weight in similarly-sized adult *Delphinus* sp., which have a brain weight of about 836 g, and an encephalization quotient of 4.2 (Ridgway 1986). In spotted dolphins from Japan, weights of body, bone, muscle and spleen are larger in males than in females (Miyazaki et al. 1981). Organ weights of spotted dolphins from Japan tend to reach growth plateaus at 2, 8-10, or 15 years, depending on the organ (Miyazaki et al. 1981).

Some body parts grow relatively faster before birth, some after. In spotted dolphins from Japan, viscera, blubber, brain, heart, lungs, liver, intestine, and spleen grow faster per unit increase in body weight before birth (i.e.,gcs are larger prenatally), while muscle, bone, kidney, pancreas and stomach grow faster (have largergcs) postnatally (Miyazaki et al. 1981).

Allometry. During postnatal development of spotted dolphins from the ETP, allometric growth pertains for most body parts (i.e., the relationship between increase in body component weight per unit increase in total body weight is curvilinear when graphed) (Edwards 1993). Only percent water in muscle and in bone exhibits isometric (linear) trends. Strong allometric growth occurs in total and metabolic surface areas of the body, and in surface area of each appendage. Moderate allometric growth occurs in maximum body diameter, average blubber depth, appendage characteristic lengths, mid-chord depths, water content of blubber, energy density of bone, and weight of blubber, muscle, bone, viscera, fins, and total animal. Weak allometric growth occurs in energy densities of blubber and muscle (Edwards 1993).

Most allometric trends, including body dimensions, are expressed most strongly during the first two or three years, consistent with achieving independence from the mother (Perrin 1975, Edwards 1993, Noren and Edwards 2007). For example, estimated muscle fraction of body wet mass increased 33% from birth to about 3 years postpartum, but only 14% from 3 years postpartum to adulthood (Edwards 1993).

Skull. In contrast to the relatively early maturity of most body components, two skull structures in spotted dolphins, the bony falx (BF) and the bony tentorium (BT), do not fully mature until several years postpartum (Nojima 1988). In many other mammalian carnivores, the BF and BT originally appear during fetal development as cartilaginous structures termed the *falx celebri* (FC) and the *tentorium cerebelli* (TC) and become fully ossified to the BF and BT form prior to birth. For example, the BF and BT are already ossified at birth in Steller sea lions, common seals, dugongs, cats, and horses. In contrast to this pattern, the FC and TC never ossify either pre- or postnally in some odontocetes (e.g., sperm and beaked whales). Two families of odontocetes, the delphinids (including spotted dolphins) and the phocoenids, display an intermediate pattern, where ossification does occur, but not until after birth. In the spotted dolphins fetus, the FC and TC are thin, transparent membranes. In immature postnatal individuals, ossification may or may not have begun. In fully mature animals, the TC and FC tend to be fully replaced by bone. The free margins of these bones are smooth and the shape is quite similar to the previous shape of the cartilaginous TC and FC. Ossification tends to begin at about one year of age and is completed, except for passage of nerves and blood vessels, by year nine (Nojima 1988).   The function of these structures in dolphins remains unexplained.

Other components of the spotted dolphins skull mature at varying rates postnatally, apparently in relation to the timing of functional importance. For example, skull components related to functions important immediately postpartum, such as respiration and acoustic processing, tend to be more mature at birth and to grow relatively

slowly postpartum, while components related to functions more important later in life, such as independent feeding, tend to be relatively immature at birth and grow relatively rapidly postpartum (Perrin 1975b).

DISTRESS, DISEASE and DEATH

The global distribution of factors affecting distress, disease and death in spotted dolphins is virtually unknown, because relevant data have been collected primarily from the Pacific Ocean, with the majority from the ETP. Most data have been collected postmortem, and most of these postmortem data were collected from dolphins killed during tuna purse-seining operations in the ETP (Dailey and Perrin 1973, Cowan and Walker 1979, Perrin and Powers 1980, Dailey and Otto 1982, Andre et al. 1990a, Andre et al. 1990b, Andre et al. 1991, Calmet et al. 1992, Cowan and Curry 2002, Romano et al. 2002a). Fewer postmortem data have been collected from spotted dolphins killed in tuna fishing nets near Taiwan (Chen et al. 2002) or stranded along the North American west coast (Worthy et al. 1993, Oliveira et al. 2011). In addition to these postmortem studies, three studies have collected data from free-ranging spotted dolphins (Romano et al. 2002b, Borrell et al. 2004, St. Aubin et al. 2011).

Postmortem data analyses can be categorized broadly as investigations of factors leading to acute death in tuna purse-seines in the ETP, or investigations of natural levels of pathologies not related to acute death in ETP tuna purse-seines, including organ diseases, parasitism, neoplasm, and contaminants. The sampling studies conducted on living dolphins include investigation of stress-related blood chemistry changes (St. Aubin 2011) and immune system responses (Romano et al. 2002b) in spotted dolphins chased, captured, released, and/or recaptured by tuna purse-seiners in the ETP, and examination of blubber organochlorine concentrations in spotted dolphins from the Coiba Archipelago west of Panama (Borell et al. 2004).

Fishery-related Acute Death.   Postmortem examination of spotted dolphins which died due to entanglement in tuna purse-seines after capture in the ETP has been carried out with two objectives: 1) to determine the proximate cause of death (Cowan and Walker 1979, Cowan and Curry 2002), and 2) to survey the general physiological condition of the animals, with respect to ongoing (subacute, presumably natural) pathologies (Cowan and Walker 1979, Cowan and Curry 2002, Romano et al. 2002b).

Cowan and Walker's (1979) examination of 4 spotted dolphins showed that 94% of animals examined had died as a result of direct contact with either the purse seine or the net enclosure of a research apparatus being utilized as a sampling device during the study. With one exception, all mortality in the purse seine fishery was directly associated with individual entanglement, canopy formation during the backdown procedure, or partial net collapse prior to backdown. Mortality occurring in the research apparatus was primarily due to individual entanglement in the net enclosure. Three young spotted dolphins (two two-tone and one speckled phase) died of undetermined causes. These young dolphins were found floating free of the net (two outside the purse seine and one inside ten minutes prior to backdown) and were externally free of net marks. One other

adult male spotted dolphin asphyxiated due to laryngeal displacement directly after tagging. In general, calves and juvenile dolphins succumbed quickly when entangled in the net, while entangled adults put up tremendous struggles prior to death (Cowan and Walker 1979).

Acute tissue changes observed in the lungs of those animals dying in the purse seine and research gear were due to asphyxiation (Cowan and Walker 1979). Violent respiratory movements associated with asphyxiation disrupt lung tissue by producing hemorrhages, alveolar and interstitial emphysema, and disseminating air emboli to liver, pancreas, kidneys, and other organs. The complex neuromuscular control of respiration in cetaceans is considered to relate primarily to exposure of the blowhole area to the atmosphere (Ridgway 1972). The resulting extraordinary degree of lung tissue damage and air emboli undoubtedly relates to struggle and to extremely powerful and violent efforts to breathe against a closed larynx. The nearest morphologic equivalent would be pulmonary laceration and bleeding in divers with the "bends", although mechanisms differ. Pulmonary alveolar rupture and bleeding is recognized in asphyxiation from many causes but "embolism resulting from interstitial emphysema is, to the best of our knowledge, unique to these dolphins. Particulate matter suggestive of water aspiration was not found (Cowan and Walker 1979). In contrast, a more recent study attributed gas emboli in gillnet bycaught marine mammals to offgassing of supersaturated blood and tissues (Moore et al. 2009). Both possibilities should be considered in future research.

Shock, or struggles related to asphyxiation, likely caused the numerous pathologies observed postmortem in heart tissue, including congestion, petechial hemorrhage, interstitial hemorrhages, and prominent "contraction banding" of myocardial and cardiac conduction fibers (Reichenbach and Benditt 1970, Cowan and Walker 1979).

The primary pathology observed postmortem in adrenal glands was extreme congestion, possibly due to the stress of capture (Myrick and Perkins 1995) but also possibly due to postmortem non-pathologic filling of the large vascular bed of the adrenals (Cowan and Walker 1979). Adrenal glands in older animals often exhibited a nodular appearance which might reflect repeated reactions to stressful events, but no other physical signs of capture or other types of stress were found (Cowan and Walker 1979).

Pathologies observed postmortem in spleens differed between younger and older spotted dolphins. Almost all spleens in adult and young adult dolphins displayed severe congestion with hemorrhages and scarring in both surface and deep (parenchymal) tissues (Cowan and Walker 1979). Splenic scars and hemorrhages were less prevalent in juveniles and calves, possibly because the older animals struggled much more violently in the purse-seine prior to death, and also possibly because older animals may have had a longer history of exposure to previous markedly stressful events. A few dolphins showed no overt symptoms (e.g., no hemorrhages, petechia, pulmonary emphysema and/or external signs of injury) and were presumed to have died of "stress," defined in this

context as a massive cardiovascular reaction to either autonomic discharge or adrenal cortical secretion or both. Cowan and Walker (1979) did not find any direct signs of fishery-related injuries likely to cause post-capture mortality. However, they did find evidence of splenic hemorrhage, which likely resulted from exposure to fishery acitivities. However, splenic hemorrhage is typically not considered a consequential lesion in most cases, as animals likely survive to form a scar and die of something else.

Cowan and Walker (1979) also considered the possibility of spotted dolphin death in purse-seines due to capture myopathy. This phenomenon has been found in stressed and captured terrestrial mammals and consists predominantly of muscle degeneration and necrosis as well as myocardial degeneration and myoglobinuric nephropathy. They found no evidence of the condition upon examination of several sites in the major swimming muscles of sampled spotted dolphins.

A second series of necropsies conducted on 28 spotted dolphins killed during ETP tuna purse-seine sets focused on much more extensive and systematic sampling of heart muscle in order to more closely examine the cardiac consequences of this fishery-related mortality and to relate those findings to the considerable body of relevant research that had accumulated since the original study (Cowan and Curry 2002). In this second study, the immediate (acute) cause of death was similar in all subject animals. All animals died with highly stereotyped findings of cardiac injury, with implied impairment of cardiac conduction, arrhythmia and muscle contractility and widespread evidence of smooth muscle spasm, including smooth muscle of small muscular arteries. All of the lesions were consistent with pathology expected from massive shock and stress reactions (Cowan and Curry 2002).

Many of the animals examined also had heart scars or other lesions that could be attributed to "stress" prior to the encirclement procedure that lead to death and which could be interpreted as resulting from a previously survived purse-seine capture experience (Cowan and Curry 2002). These signs included small patchy myocardial scars and abnormalities of small vessels consistent with mural injury due to spasm and also microthrombi in the process of organization, or the presence of small plaques that are thought to result from endothelial injury and local thrombosis. These results imply that some animals experience cardiac injury of such a degree that they die in the nets, while other animals who suffer similar injury, but to lesser degree, survive either to resolve the lesions without scar, or replace damaged tissue with scar tissue. One spotted dolphin known to have been set on and caught more than once prior to death had similar lesions to those found in animals dying in fisheries operations, indicating that fisheries animals could have been set on more than once and survived (Cowan and Curry 2002).

The major findings relating to acute reactions were observed in the myocardium (Cowan and Curry 2002). Hearts were found to be blotchy, indicating circulatory disturbance, and consistently affected with microscopic changes including fiber changes, perinuclear vacuolation, and contraction band necrosis. Numerous indications of prolonged coronary artery spasm also were observed in various circulatory tissues and

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organ systems, leading Cowan and Curry (2002) to conclude that "the cause of death of the dolphins dying in the purse-seines was acute endogenously generated myocardial injury, leading to arrhythmia and sudden death". The overall patterns of pathologies observed postmortem appear to result from a stereotypic stress response, activating all the physiologic adaptations to diving or escape to an extreme or pathological level, resulting in widespread ischemic injury to tissues (Cowan and Curry 2002). This conclusion is supported by catecholamine concentrations measured in one of the sampled animals. Levels of epinephrine, nor-epinephrine and dopamine were all roughly an order of magnitude greater than the maximum values obtained for any living dolphins subjected to capture by purse-seine (St. Aubin 2002).

The pathological changes observed in ETP spotted dolphins expiring in tuna purse-seines are similar to those observed postmortem in the organs and tissues of a variety of beach-stranded, net-caught, and captive small odontocetes (Cowan and Curry 2008).   The observed injuries indicate "multi-systemic injury caused by a massive release of endogenous catecholamines or vasospasm leading to ischemic injury, followed by reperfusion and reperfusion injury" (Cowan and Curry 2008). These findings indicate that odontocetes generally respond reflexively to perceived danger with a pervasive alarm reaction that involves increasing physiological adaptations for diving or escape to a pathological level, which if significantly prolonged results in widespread ischemic injury. The unavoidable nature of these reflexive alarm responses may be the underlying basis not only for the frequent mortality of beach-stressed and/or transported/handled dolphins (Cowan and Curry 2008) but also those subjected to prolonged entrapment in tuna purse-seine nets.

Fishery Effects on Blood Chemistry. Hematology, serum chemistry, and plasma hormones were examined in living spotted dolphins after chase, capture, and sometimes recapture by tuna purse-seiners in the ETP (St. Aubin 2002, St. Aubin et al. 2011). Blood was collected from 72 dolphins, of which 55 were presumed captured for the first time. Seventeen blood samples were taken from dolphins recaptured one or more times. Inter-individual variability and small re-sample sizes precluded determination of population-level long-term responses to repeated chase and encirclement. However, blood chemistry analyses indicated physiological adjustments consistent with a measurable stress response typical of odontocetes. In particular, blood catecholamine, cortisol and ATCH levels were elevated above values expected in non-stressed odontocetes, and the general magnitude of the physiological stress response was greater than found in bottlenose dolphins subjected to capture and release without a prolonged chase period. Enzymes typical of muscle damage following exertion were moderately elevated but below levels expected to cause long-term muscle damage or sustained muscle necrosis.

Some blood parameters (platelet, white blood cell and eosinophil counts, and mean cell hemoglobin concentration) showed apparently stress-related changes with length of time under stress, while other parameters (serum creatine kinase, thyroid (T4) and globulin) were significantly decreased in dolphins recaptured after 1-3 days. Overall, stress responses were observed in all dolphins tested. Responses were within ranges observed

in other wild mammals; levels were generally higher than in non-stressed animals but lower than levels observed in dolphins following apparently stress-related death (e.g., during tuna purse-seine nets, or following stranding) (St. Aubin 2002, St. Aubin et al. 2011).

Fishery Effects on Immune System Morphology and Function. Immune system responses to ETP purse-seine fishery activity have been investigated through examination of lymphoid tissues collected from spotted dolphins killed in the fishery (Romano et al. 2002a) and lymphocytes collected from peripheral blood of live spotted dolphins after chase and capture (Romano et al. 2002b). Immune system responses to fishery activity may be expected based on recognition that stress in mammals can bring about changes in immune morphology and function (Romano et al. 2002a).

Lymph Tissues. Spleen, lymph nodes, thymus, and gut-associated lymphoid tissue were collected from 30 spotted dolphins, 24 *Stenella longirostris*, and 2 *Delphinus delphis*, in order to gain an understanding of the effects of repeated chase and encirclement on the immune system in these dolphins (Romano et al. 2002a). The investigation included examination of lymphoid organ morphology as well as autonomic enervation of lymphoid organs, based on the observation that anatomical links between nervous and immune systems "establishes a pathway whereby stress as "perceived" by the brain can affect immunocompetence". Findings were similar for all three species. Lymph organs appeared healthy with no stress-induced involutions of lymph tissue in the sample of animals examined. An anatomical link whereby stress-related chemicals could affect immunocompetence was observed between the brain and the immune system, involving close associations between cells of the immune system in the spleen and mesenteric lymph nodes. The spleen of adult dolphins was typical of other mammals, although the spleen of one newborn (< 80 cm total length) spotted dolphin displayed different organization than that observed in older dolphins. In general, the neonate spleen was less organized, perhaps implying greater susceptibility to infectious agents. Lymph nodes from all dolphins appeared to be relatively normal and actively functioning, although nematodes and larvae were found in two dolphins. The thymus was similar to other mammals, and the gut contained associated lymphoid tissue as expected. Abundant autonomic enervation exists in thymus, spleen and mesenteric lymph nodes, further establishing an anatomical link between the nervous and immune systems in ETP dolphins, whereby "neurotransmitters released during stress may affect the immune response as well as lymphocyte trafficking" (Romano et al. 2002a). However, overall there was no morphological indication of immune system compromise in the fishery-killed dolphins.

Immune Characteristics of Peripheral Blood. Because "evidence from a variety of disciplines supports bi-directional communication between the nervous and immune systems", three aspects of immune system characteristics in peripheral blood samples were examined in living ETP spotted dolphins, including: "1) percentages and numbers of *lymphocyte subsets* (including T helper cells, T cells, B cells, and MHC class II+ cells) from first time chase and encircled dolphins vs. repeat chased and encircled dolphins, by

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lymphocyte immunophenotyping and flow cytometry, 2) degree of *lymphocyte proliferation* in first time chase and encircled dolphins vs. repeat chased and encircled dolphin, by the mitogen proliferation assay, and 3) degree of *DNA damage* in white blood cells from first time chase and encircled dolphins vs. repeat chased and encircled dolphins, by the comet assay" (Romano et al. 2002b). T cell lymphocytes include T helper cells that help the immune response and T cells that destroy host cells infected with intracellular pathogens, including viruses. B cell lymphocytes produce antibodies that destroy extracellular pathogens and their products (Romano et al. 2002b).

Lymphocyte subsets. The ETP study provides the first measurements of T, B and T helper cell lymphocyte percentages/numbers, MHC Class II expression, and T/Thelper cell ratios in spotted dolphins (Romano et al. 2002b). T cells, T cell percentages, and T/B cell ratio increased significantly, while B cells, B cell percentages, and total lymphocytes decreased significantly, from first capture to recapture. Analysis of the first capture group showed gender differences, with males having significantly higher T cell counts, T helper cell counts, and MHC class II+ counts, than females. Analysis of the first capture group also showed age-related differences, with significantly higher percentages of T cells and T helper cells, and significantly lower B cell percentages, in mature vs. immature dolphins. Immature dolphins showed significantly higher absolute numbers of lymphocytes, MHC class II+ cells, and B cells.   In general, the ranges of B, T, and T helper cell measurements from spotted dolphins were similar to ranges observed in healthy bottlenose dolphins at rest. No significant differences in lymphocyte proliferation were found between first and repeat captured groups, male vs. female dolphins, or mature vs. immature dolphins. No significant differences were found in DNA damage between first and repeat captured groups, or male vs. female dolphins.   In general, the immune system studies indicated moderate responses by some elements of the system, similar to those found in other studies of the effect of stress on the immune system, but no significant overall changes in immune function, although larger sample sizes taken over longer periods might reveal larger effects (Romano et al. 2002b).

Non-Fishery-Related Disease and Death.   Postmortem examination of spotted dolphins killed in ETP tuna purse-seines has provided a number of insights regarding natural (non-fishery-related) levels of pathology in spotted dolphins, including organ diseases, parasitism, cancer, and contaminants.

Organ Diseases. Studies of disease prevalence in spotted dolphins are rare, as is the incidence of disease in the animals studied. Two studies have examined disease factors in spotted dolphins killed during tuna purse-seine sets in the ETP (Cowan and Walker 1979, Cowan and Curry 2002), two studies report the presence of vaginal calculi in spotted dolphins from the ETP fishery (Sawyer and Walker 1977, Cowan and Walker 1979), and Worthy et al. (1993) present necropsy findings for a spotted dolphin stranded on the northern coast of California, USA .

The lungs are the organs most frequently and most extensively involved in natural disease processes, with most involvement due to the lungworm, *Halocercus delphini,* as

discussed in the section on parasites. Only a few specimens have exhibited organic problems other than parasitism (Cowan and Walker 1979, Cowan and Curry 2002). Evidence of vascular disease (irregular thickening of walls of small arteries and arterioles) was found in two spotted dolphins. One of these dolphins also had small foci of degeneration and scarring of the myocardium. Three instances of minor focal myocarditis and two of "basophilic degeneration" were found, along with scattered foci of inflammation in the kidneys and livers of these animals. Evidence of significant fiber fragmentation or fiber regeneration was not found (Cowan and Walker 1979).

With the exception of two instances of bile duct parasitism by trematodes and a few instances of small scattered foci of inflammation, no chronic liver disorders were found (Cowan and Walker 1979). Aside from parasitism, all intestinal tracts and air sinuses were normal. Findings of pre-existing (prior to fishery demise) disease in kidneys included three cases of focal interstitial inflammation, one animal with an infarcted reniculus, several instances of isolated glomerulosclerosis and arteriosclerosis, and a single occurrence of a small simple cyst. A neoplasm of tubular epithelial origin was found in an animal which also had a pancreatic tumor (Cowan and Walker 1979).

Other than two cases of parasitism, the only disease process associated with reproductive organs was the appearance of vaginal calculi (Sawyer and Walker 1977, Cowan and Walker 1979). The structures tend to be roughly pyramidal in shape, variable in size (approximately 1-1.5 cm in diameter), and composed of calcium phosphate compounds with lower concentrations of various minerals, but no uric acid or fluoroxalate; i.e., compounds identical to mammalian bone. Cross-sections indicate that the calculi are formed by concentric layer crystallization for an unknown time period (Cowan and Walker 1979). Similar calculi in sexually mature *Delphinus* appeared to originate from fetal skeletal remains, leading to an hypothesis that the calculi represent spontaneous incomplete abortion (Woodhouse and Rennie 1991).

A few specimens of spotted dolphin from the ETP have exhibited splenic changes suggestive of reaction to some infectious agent (Cowan and Walker 1979). These changes consisted of enlargement, softening, and prominent follicular reaction, which in one animal was associated with follicular necrosis. These changes did not correlate with either parasitism or evident lung inflammation and did not appear to have any relation to the fishery (Cowan and Walker 1979).

A relatively common finding was small, often multiple, foci of chronic interstitial inflammation in the kidneys (Cowan and Curry 2002). These conditions were not considered to be a significant mortality factor. This background of disease is almost trivial when compared with parasitic disease found in some in-shore populations. In general, spotted dolphins inhabiting the ETP appear to be generally healthy, with adequately functioning immune systems, evidenced by low levels of infectious and parasitic disease, although this assessment was based on relatively small sample sizes, so that conditions occurring with low frequency (less than 1-2%) are unlikely to have been observed (Cowan and Walker 1979, Cowan and Curry 2002).

A sexually mature female coastal spotted dolphin (*S.a. graffmani*, 202 cm, 71 kg) live-stranded near Santa Cruz, CA in May 1989 but perished within several hours (Worthy et al 1993). External examination revealed numerous healed cookie-cutter shark bites and several recent sets of tooth rake marks. The stomach was empty. Hematology analysis and necropsy indicated elevations in ALT (alanine aminotransferase) and bilirubin suggestive of liver disease and elevated white blood cell count, alkaline phosphatase and sedimentation rate, suggestive of general infection. High levels of *Micrococcus* and low levels of gram negative bacteria were found in the blowhole. A large number of larval cestode cysts, especially *Monorygma delphini,* were found in the mesentaries, as well as *Phylobothrium delphini* in the blubber. Suggested cause of death was respiratory and cardiovascular collapse due to the cumulative effects of parasitism, necrosuppurative dermatitis and cellulitis, lung and liver pathology, and possibly hypothermia (Worthy et al. 1993).

Parasitism. Parasitism is the most common and widespread naturally-occurring disease factor in spotted dolphins from the ETP (Cowan and Walker 1979, Cowan and Curry 2002). Ectoparasites and commensals of spotted dolphins include a cyamid amphipod *Syncyamus sp.* (Perrin et al. 1987) and the barnacles *Conchoderma auritum* (Perrin 1969) and *Xenobalanus globicipitus* (Ross 1984, Oliveira et al. 2011). Endoparasites are extremely common in the spotted dolphins examined to date, particularly various types of worms including nematodes (roundworms), trematodes (fluke-type flatworms, characterized by a thick outer cuticle and one or more suckers or hooks for attaching to the host), cestodes (tapeworm-type flatworms characterized by a long flat body with an organ of attachment at one end), and acanthocephalans (spiny-headed worms, characterized by a cylindrical, retractable proboscis that bears many rows of hooked spines) (Dailey and Otto 1982). Certain species of these parasites tend to occur in specific areas of the body in spotted dolphins. For example, the cestode *Phyllobothrium* tends to occur in blubber, the nematode *Anisakis* is found in the stomach and the trematode *Nasitrema* tends to be found in respiratory structures (Perrin et al. 1987, Oliveira et al. 2011).

Parasitism by various organisms can vary with the age of the host and may affect mortality rates. The percentage of spotted dolphins in the ETP infected with the stomach worm *Anisakis* increases with age from neonates to calves to subadults, but decreases in adults, indicating that "either some reduction in number of worms occurs in a heavily-infected porpoise as it matures, …, or that heavily-infected individuals die before attaining maturity" (Dailey and Perrin 1973). Similarly, examination of skulls from the ETP and from museum collections indicates that rate of infection with *Crassicauda*-type parasites is strongly age-related (Dailey and Perrin 1973, Perrin and Powers 1980). The percentage of skulls with lesions increased from less than 5% in neonates (no dental layers) to about 20% in dolphins with about 5 dentinal layers (probably calves), then decreased again to about 10% in dolphins with about 8 dentinal layers (probably subadults), and to less than 5% in dolphins with 14-16 dentinal layers (probably mature adults). The most severely damaged skulls were from calves. The bone changes caused by the worms were so extensive that observable signs would remain in adults even if

partially healed.   Because no signs of healing were observed in adults, the data imply that severe *Crassicauda*-type infestation in calves contributes to natural mortality in those affected calves (Dailey and Perrin 1973). If dentinal layers are deposited once per year, the rounded estimates of nematode-induced mortality are 1% per year for animals with 8 or more layers, and 3% per year for those with more than 5 layers. Thus, worm infestation may be an important mortality agent for some ages of spotted dolphin, given that estimated total annual natural mortality of ETP dolphins is 7-9% per year (Perrin and Powers 1980).

In a similar age-related pattern, non-larval cestodes *Tetrabothrium forsteri* and *Strobiliocephalus triangularis* were found in greatest numbers and frequencies in calves, and calves and subadults, respectively. *S. triangularis* infested two calves and two subadults to the point that the last meter of intestine was all but blocked and swollen three to four times its normal diameter, but the parasite was not found in any adult examined. In a contrasting age-related pattern of parasitism in spotted dolphins in the ETP, cysts of the cestodes *Monorygma* and *Phyllobothrium* were rarely found prior to subadult age, yet were found in 100% of adults examined. Infection rates of spotted dolphins from the ETP by the four parasite species (*Monorygma grimaldi* (serosa), *Phyllobothrium delphini* (blubber), *Strobilocephalus triangularis* (lower intestine), and *Crassicauda sp*. (air sinuses and mammary glands) have been reported by Dailey and Perrin (1973) and Cowan and Walker (1979). *Crassicauda sp*. occurred in 33% of calves and 12.5% of subadults (Cowan and Walker 1979); details of other infestation rates were not reported. Incidence of the lungworm, *Halocercus delphini*, was much higher in Cowan and Walker's (1979) study (37%, 85%, and 46% in calves, subadults, and adults, respectively) than in the earlier study by Dailey and Perrin (1973) (15%, 15% and 0%), perhaps because Cowan and Walker (1979) included histological in addition to gross morphological examination, with the result that the lungs were found to be the organ most frequently and most extensively involved in natural disease processes (Cowan and Walker 1979). Lungworm infestation was also "especially prevalent" in 28 spotted dolphins from the ETP necropsied during an examination of stress responses due to fishery activities (Cowan and Curry 2002). Most lung lesions were attributable to *H. delphini* based on recognition of viable worms or degenerated fragments of worms in foci of inflammation and also by scarring (Cowan and Walker 1979).

However, not all lesions were proven to be caused by lungworm. The incidence of lung lesions is far greater than this, and in a given animal both lesions with and lesions without demonstrable worm fragments may be found. It appears likely that all adult spotted dolphins from the ETP will have some scarring in the lungs. Comparison of lesions of obviously differing ages revealed that the dolphin's inflammatory reaction leads to death and ultimate fragmentation of the lungworm. Some worm fragments mineralize, while others simply become more and more indistinct. Because of this, it is likely that a far higher proportion of lesions are actually caused by worms than can be shown to contain worms (Cowan and Walker 1979).

The evolution of the worm-associated lung lesion is fairly stereotyped. An acute suppurative reaction occurs in the bronchiole surrounding the worm and is relatively confined by the structural muscle and cartilage (Cowan and Walker 1979). The bronchiole is occluded and the distal segment, including acini and alveoli, either fills with exudate or collapses. Lesion development results in necrosis of tissue, including muscle and cartilages, and dissolution of the worm rather than enlargement of the inflammatory area. Lesions typically remain a centimeter or smaller in diameter, although adjacent lesions may become confluent producing a larger irregular mass. Debris may be removed through liquefaction or may calcify. In extreme examples, metaplastic ossification may result. In cases in which larvae are present, the histopathologic pattern is different. *Halocercus delphini* is viviparous, with first-stage larvae normally discharged into large air passages (Delyamure 1955). Aspiration may cause the larvae to enter the alveoli, where they excite a marked inflammatory reaction. Patches of diffuse pneumonitis are commonly associated with clusters of larvae, perhaps because of their small size and ability to permeate the air spaces. The ultimate fate of the larvae is unknown, but the vigor of the tissue reaction against them suggests they succumb quickly. In addition to lesions caused by worms, and nodules histologically identical to them, patches of pneumonitis and mucinous edema were not uncommon (Walker and Cowan 1979).

Most other organs of spotted dolphins, at least those from the ETP, exhibit relatively little parasitism. Liver parasitism has been observed rarely, including only two instances of bile duct parasitism by trematodes and a few instances of small scattered foci of inflammation (Cowan and Walker 1979). The trematode worms were identified in sectioned tissue and therefore were not readily identifiable to species. Dailey and Perrin (1973) did not report bile duct parasitism in spotted dolphins from the ETP. Tissue reaction to the parasites was typical, showing localized proliferation of biliary epithelium associated with irritation. Intestinal tract parasitism occurs infrequently (Cowan and Walker 1979, Oliviera et al. 2011). Examination of three one-meter lengths of intestine from ETP spotted dolphins, taken just posterior to the duodenal end, at mid-length, and at the posterior end of the intestinal tract, revealed only one instance of parasitism; presence of the cestode *Strobilocephalus triangularis* occurring exclusively in the rectal area with the scolex of the worm encapsulated deep in the intestinal wall (Cowan and Walker 1979). Tissue reaction to these worms was a mild, localized, low-grade inflammatory response (Cowan and Walker 1979). Air sinuses of spotted dolphins from the ETP are infested with the nematode, *Crassicauda sp.* at a rate of about 10% (Dailey and Perrin 1973, Cowan and Walker 1979). The pancreas and hepatopancreatic ducts of spotted dolphins from the ETP are occasionally infested with trematodes (Cowan and Walker 1979), including *Campula rochebruni* and *Zalophotrema pacificurn* (Dailey and Perrin 1973, Gibson and Harris 1979). These tissues react to trematode infestation with a mild inflammatory response, i.e., cellular proliferation typical of localized irritation. The mammary glands of adult spotted dolphins from the ETP are occasionally infested with the nematode *Crassicauda* with minimal host inflammatory response (Cowan and Walker 1979).

Necropsy of two spotted dolphins from the Puntarenas area of western Costa Rica reflected parasitism patterns found in other studies, reporting Tetraphyllidean plerocercoids (anal crypts), *Anisakis* sp. (stomach), and *Halocercus* sp. (lungs) in a juvenile male, and *T. foresti* (intestine), *M. grimaldi* (testis), *N. globicephalae* (air sinuses), trematode eggs (lungs), *Anisakis* spp. (stomach), and *X. globicipitis* (skin of caudal fluke) in a senile male (Oliveria et al. 2011).

Neoplasms. There is one reported case of an immunoblastic malignant lymphoma in a one-year-old female spotted dolphin stranded in south Florida (Bossart et al. 1997). . She was one of 5 dolphins (3 *Tursiops trucatus*, 1 *Stenella frontalis*, and 1 spotted dolphins) from the south Florida area diagnosed over a two-year period with similar lymphomas, which are generally rare in cetaceans (Bossart et al. 1997). The authors suggested genetic, environmental, and/or infectious etiologies as causative factors for this cluster of lymphomas.

Contaminants. A variety of contaminants have been found in spotted dolphins from a variety of areas, including cadmium (Cd) (Andre et al. 1990a), mercury (Hg) (Andre et al. 1991), lead (Pb), cesium (Cs), and potassium (K) (Calmet et al. 1992) in spotted dolphins from the ETP; mercury and selenium (Se) in spotted dolphins from Taiwanese waters (Chen et al. 2002); and organochlorine compounds in spotted dolphins from the eastern coast of South Africa (Cockroft and Ross 1991), Australia (Kemper et al. 1994) and the west coast of Panama (Borell et al. 2004).

Cadmium *concentration* indicates which organs tend to retain Cd most actively, and was highest in the kidney (48.7 mg kg^{-1}), then liver (8.72 mg kg^{-1}), with other organs containing 1-5 mg kg^{-1}, and the lowest concentrations being found in brain and muscle (Andre et al. 1990a). Cadmium *burden* is affected by total weight of the body, and reflects accumulation in general. Due to the large fraction of body weight comprised of muscle and intestine, 85% of the overall body burden (total concentration in various body parts) occurred in the liver, kidney, muscle and intestine, in approximately equal parts (Andre et al. 1990a).

Cd *concentration* increased significantly (P<0.05) with *age* in muscle, stomach, intestine, spleen, skin, brain, heart, and pancreas (Andre et al. 1990a). Cd *burden* increased with *age* in liver, kidney, muscle, stomach, intestine, brain and heart. Cd *concentration* increased significantly (P<0.05) with *total wet weight* in kidney, stomach, intestine, heart and pancreas, while Cd *burden* increased significantly with *total wet weight* in liver, kidney, muscle, stomach, and intestine. Cadmium levels were significantly affected by gender in four cases, three involving Cd concentration and Cd burden in intestine vs. animal weight, and the fourth involving Cd burden in spleen vs. animal age. Cd was higher in females in these 3 cases. In the fourth case (Cd burden in spleen), Cd was greater in males. Sampled males were heavier than females, but it is not known whether this weight difference is related to these gender patterns in Cd (Andre et al. 1990a).

Cd contamination was highest in spotted dolphins from the northeastern ETP and lowest in dolphins captured nearest the equator and farthest from the coast of California (Andre et al. 1990a). Year of capture appeared to be important despite the small number of animals sampled, with lower concentrations and burdens of Cd found in 1977 than in 1983. Average Cd concentration in spotted dolphins from the ETP tended to be somewhat higher than concentrations in Japanese animals (0.03-0.63 vs 0.01-0.25 mg kg^{-1} muscle; 0.17-37.8 vs 0.04-0.11 mg kg^{-1} liver, 0.60-94.7 vs. 0.06-69.6 mg kg^{-1} kidney). The Cd distributions and concentrations from ETP spotted dolphins indicate long-term, low-level contamination, primarily through ingestion of contaminated prey. Most non-intestinal Cd is apparently processed through and eliminated by the liver, while long-term accumulation appears to be occurring in the kidneys (Andre et al. 1990a).

Calmet et al. (1992) measured ^{210}Pb, ^{137}Cs, and ^{40}K in muscle and liver of spotted dolphins killed during tuna purse-seine sets in the ETP between 80°W-135°W x 180°N-13°S, during the years 1977-1983. Spotted dolphin specimens averaged 10 yrs of age, 180-181 cm total length, and 55-62 kg total wet weight. ^{137}Cs averaged 1.19 (s.d. 0.54) in liver and 1.74 (s.d. 0.60) in muscle. ^{40}K averaged 331 (s.d. 61) in liver and 432 (s.d. 73) in muscle. Muscle/liver ratio of ^{137}Cs was 1.74 (s.d. 0.93). The higher concentrations of both ^{137}Cs and ^{40}K in muscle compared to liver were significant in both cases. ^{210}Pb was detectable in only 9 muscle samples and 22 liver samples, but was significantly higher in liver than muscle (2.1 mBq kg^{-1} vs. 0.5 mBq kg^{-1}, respectively), presumably reflecting a higher accumulation rate of trace metals in the liver. Principal components analyses indicated that highest concentrations of ^{137}C occurred in younger animals netted farthest west, in the northern hemisphere at the earliest year. This pattern is consistent with aerial contaminant patterns resulting from fallout due to atmospheric nuclear testing in the western Pacific in the 1950s and early 1960s. Higher levels of ^{137}Cs were found in female spotted dolphins compared to all spotted dolphins sampled. Estimated concentration factors (CFs) from seawater to spotted dolphins muscle ranged from 30-100, similar to CFs found for ecologically similar fish such as tuna (Folsom et al. 1967, Susuki et al. 1973). Overall, dose rates from internal sources (i.e., ingested food) were much higher than ^{137}Cs dose rates from external sources, but both were much lower than the natural background dose rate due to ^{40}K. Estimated dose rates of ^{210}Pb were negligible relative to the natural background dose, so overall it appeared very unlikely that exposure to either ^{137}Cs or ^{210}Pb has had any effect on ETP dolphin populations (Calmet et al. 1992).

Andre et al. (1991) studied Hg contamination in spotted dolphins from the ETP and concluded that the Hg was of natural (rather than anthropogenic) origin and accumulated through trophic transfers. It is more likely that mercury contamination in the ETP results from diet rather than from cutaneous or pulmonary absorption, because ambient mercury levels are low in ocean water as well in most atmospheric regions in the ETP. Trophic absorption of Hg is dependent on the Hg being in methylated form, as found in most of the prey (fish and squid) consumed by the dolphins. Once absorbed into the bloodstream the Hg passes to the various organs. Hg can be eliminated in urine, feces, and maternal milk, as well as by crossing the placental barrier and accumulating in

a developing foetus. Total Hg concentration and burden was highly correlated with latitude of capture for all body parts except blood, melon and subcutaneous fat. In every case, mercury accumulation increased with proximity to the equator. The increase may result from increased atmospheric mercury, perhaps resulting from biological activity of algae and bacteria converting dissolved inorganic mercury into volatile chemical forms. Longitude was never a significant factor. Concentration of Hg in the liver   (67.73 mg kg^{-1}) was several times higher than in spleen (10.29), blubber (7.6) or kidney (5.21). Concentration ranged between 1-5 mg kg^{-1} in all other body parts measured. Average body burden of Hg was highest in blubber (109.76 mg), then liver (85.68) and muscle (76.47). These three components accounted for 95% of total body burden. Hg concentration in lungs and intestines averaged 5.88 mg and 3.66 mg. Average burden in other organs was less than 2 mg Hg. Hg concentrations and burdens were unusually high in certain individuals, e.g., 217 mg kg^{-1} in one liver sample, 30 mg kg^{-1} in one muscle sample (vs. 2.27 average concentration), and 1.4 mg kg^{-1} in one blood sample (vs. 0.36 average concentration) (Andre et al. 1991).   Hg tended to accumulate with age in most, but not all, body parts.   Perhaps because animals younger than 3 years of age were eliminated from the analysis (due to small sample size), Hg concentration in kidneys, heart, skin and blubber, and Hg burden in the heart were not significantly related to age. Hg concentration was greater in females than males in liver, kidney, muscle, stomach, intestine, spleen, lungs, skin, and pancreas (Andre et al. 1991). The basis for these various patterns in Hg characteristics is unknown.

In Taiwanese waters, spotted dolphins muscle (collected at the flank under the dorsal fin, Chen et al. 2002) contained 3.64 mg total Hg kg^{-1} and 2.81 mg organic Hg (O-Hg) kg^{-1}. These values were similar to concentrations in *Grampus griseus*, and significantly higher than in *Stenella longirostris* or *Tursiops truncatus*. Total Hg and O-Hg, but not Se, increased with body length in spotted dolphins. Unlike in Andre et al's 1991 study, no gender differences were found in any measure.   In spotted dolphins, the rate of accumulation of total Hg appeared to decrease at about 4 mg kg^{-1}.   Average total Hg in Taiwanese waters was 1.5 and 3.0 times higher than in ETP or Australian waters, respectively (Andre et al. 1991, Kemper et al. 1994, Chen et al. 2002).

Mean concentrations of the organochlorine compounds HCB, tPCB, and tDDT in blubber samples from spotted dolphins from the Coiba Archipelego Panama were 0.064, 2.30 and 6.4 mg kg^{-1} wet weight, respectively (Borell et al. 2004). These levels are not considered a threat to spotted dolphins. These organochlorines are lipophilic, concentrate through food chains, and are especially likely to concentrate in dolphins because they are top predators, they have a thick hypodermic fat layer, and they have a relatively high metabolic rate (compared to other cetaceans). Overall, tDDT was 3 times higher than tPCB (6 vs 2 mg kg^{-1}); HCB was negligible. No gender differences were observed in organochlorine concentrations or PCB profiles, which is unexpected because adult males usually accumulate organochlorines steadily while females reduce their burden through transfer to offspring during gestation and nursing. The observed ratio of DDT/tPCB (2.69) indicates that dolphins in the area (the western coast of Panama) are exposed to organochlorines through agrarian (application of DDT as a pesticide) rather than

industrial activities. The PCB profile differed significantly between school 5 (14 animals sampled) and school 6 (26 animals sampled), despite being sampled only 9 days and 20 miles apart. This difference between schools suggests different exposure histories and may imply strong school or site fidelity (Borell et al. 2004).

Concentrations of the organochlorine compounds PCB and DDT in 4 spotted dolphins from the eastern coast of South Africa ranged from 4.77-48.3 and 5.79-65.2 mg kg^{-1} wet weight, respectively (Cockroft and Ross 1991). These levels are much higher than observed off the coast of Panama (Borell et al. 2004), presumably reflecting a much larger rate of anthropogenic input. Concentrations of PCB, CCt, and HCB in a single spotted dolphin from Australia were much lower (0.82, 1.19, and 0.009 mg kg^{-1} wet weight, respectively) (Kemper et al. 1994), presumably reflecting a much lower rate of anthropogenic input.

IMPLICATIONS FOR FISHERY EFFECTS

The spotted dolphin is in many ways a "typical small cetacean", being a relatively small (about 2m long and about 75kg wet weight), hydrodynamically optimized, obligate marine carnivorous mammal with a relatively wide geographic distribution and some local variation in morphology. However, within this "typical" framework a number of physical characteristics exist that may predispose the species to suffer adverse effects during their common interactions with tuna purse-siener activities in the ETP. Potentially troublesome characteristics are discussed by system below.

Acoustic System. Morphology and performance of the spotted dolphins acoustic system appears similar to that of other Type II odontocetes, with acoustic signals produced by spotted dolphins in the ETP ranging between about 3 kHz and 150 kHz.   Surprisingly, no studies have investigated the acoustic environment produced by tuna purse-seiner activities, or the manner in which these activities may interfer with dolphin sound production and reception during purse-seine sets. Noise associated with tuna purse-seine sets in the ETP is considerable and will emanate from many sources, including the searching helicopter, the seiner, the net skiff, the speed boats, the propellers and movement of water associated with each vessel, and the crewmen and divers working the net and the various vessels during the set.   The extent to which purse-seiner-associated noise interferes with these frequencies, and the effect of distance on any interference, is unknown but potentially significant and remains to be examined.

Cardiovascular and Muscular Systems: The cardiovascular system of spotted dolphins appears generally similar to that of other delphinids, although metabolic enzyme activities in various body parts indicate that this delphinid may be particularly adapted to sprinting rather than long-term sustained high speed swimming. For example, the high levels of LDH and PK activity in skeletal muscle, the unusually high buffering capacity of the swimming muscle, plus the high activity of CS in brain and heart, are similar to adaptations for short-term high activity (i.e., sprinting) observed in rabbits. In addition, heart mass in spotted dolphins is relatively smaller than in several other delphinids. Taken together, these adapatations imply a lesser capacity for sustained high-energy

activity, such as that required during prolonged evasion of tuna purse-seines both pre- and post-capture. Smaller, younger spotted dolphins are likely to be at greatest risk, given their proportionally reduced muscle mass and likely underdeveloped respiratory capacity and muscle physiology. More samples and studies are warranted to address this question.

Development: The acoustic system of perinatal spotted dolphins differs from adults in having a smaller eighth cranial nerve and no second channel of fatty tissue lateral to the TPO complex. These differences may imply reduced ability to process acoustic signals perinatally, which could interfere with communication between young spotted dolphins and adults during tuna purse-seine set evasion. Acoustic modeling studies would be helpful to examine this issue.

Digestive System: The digestive system of spotted dolphins is generally similar to that of other delphinids, but may be particularly susceptible to intestinal volvulus (bloat) due to its unusually long intestine. Intestine length may contribute to the observed problem of volvulus in a close relative of spotted dolphins, Stenella clymene (Anderson and Rawson 1997). Out of 235 stranded cetaceans (197 Tursiops sp, 19 Stenella clymene, and 1-5 each of 9 other species), the only 3 found to have died due to necrosis of the intestine were three specimens of Stenella clymene. Death was believed to have been caused by mesenteric compression, specifically by volvulus, which involves twisting of a loop of intestine about its mesenteric base of attachment (Rosen et al. 1988). Athough the intestines were not twisted when examined, the affected animals were all young and the bowel tends to be especially mobile in younger animals.   This condition is analogous to colic in horses and bloat in dogs. It likely results from violent and/or rapidly twisting movements of the body, such as the high leaps and/or spinning during fast swimming characteristic of spotted dolphins (Anderson and Rawson 1997). This propensity for bloat implies that uncharacteristically large leaps or other avoidance maneuvers by young spotted dolphins evading tuna purse-seine sets may produce a higher than normal possibility of bloat-induced mortality. The problem remains to be investigated.

Distress Disease and Death: It appears that younger spotted dolphins are more likely than older individuals to succumb quickly to stress-related death. Calves and juveniles reportedly succumb quickly when entangled in nets, compared to entangled adults that survive longer with prolonged stuggling prior to death. Dolphins found dead in the net with no obvious cause tend to be young animals. All forms of hemorrhages are more common in adults than young dolphins, perhaps due to the more vigorous and/or longer sustained pre-mortem struggle by adults.   Splenic hemorrhages have been found in some young dolphins, and the underdeveloped spleen characteristic of neonate spotted dolphins may be more susceptible to infection, implying that spleenic damage may occur more quickly with less provocation in young spotted dolphins compared to adults. Less-developed lymphocyte subset composition in younger animals may also predispose younger spotted dolphins to more damage from a given stimulus than would be the case for an adult. Potential interactions between immune function, age, and stresses related to tuna purse-seine set evasion remains to be investigated.

Parasitism. Several parasites are age-specific in specimens of spotted dolphins collected from the ETP. For example, the incidence of *Anisakis* (stomach nematode worm) and skull lesions due to *Crassicauda* (nasal sinus nematode worm) increases from from neonate to calf to subadult but decreases in adults, implying age-specific mortality related to parasitism by these nematodes. Similarly, the incidence of non-larval intestinal cestodes was highest in calves and subadults, occluding the last meter of intestine in some individuals, but was never found in adults, presumably because the highly-parasited individuals would not survive to adulthood. The potential effect of parasitic load on age-specific spotted dolphin survival, due to the added stress of tuna purse-seine set evasion, remains to be investigated.

In a contrasting pattern, lungworm and cestode infestation increases with age in spotted dolphins*,* so that by adulthood, 100% of dolphins retrieved from areas of tuna seining operations are affected. The increase in lungworm infestation probably occurs because the lungworm larvae occur in large air passages, so that aspiration during breath intake can drive larvae into the alveoli, where they cause a marked imflammatory response. The effect of this worm infestation on lung function should be investigated to determine whether changes in respiratory efficiency occur such that the prolonged evasion response associated with tuna purse-seine sets negatively impacts spotted dolphin survival.

External Characteristics.   Spotted dolphin integument is typical of that of other small delphinds, having an outer layer of infection-resistant skin protecting a blubber layer of variable content and thickness below.   Stress reactions may diminish this infection resistance and thus may affect survival rates.   Spotted dolphins'relatively thin blubber layer compared to small cetaceans from more temperate regions (e.g., *Phocoena phocoena*) may contribute to enhanced heat flow, although prolonged exercise by spotted dolphins in the ETP has been observed to increase skin temperature in adult dolphins, implying that heat flux may become a problem at some point. This will be especially true if, as is the case for *Tursiops truncatus*, the lowest thermal conductivity of blubber is found in calves and pregnant females. Heat flux modeling would be useful to address this possibility.

The external morphology of adult spotted dolphins is highly adapted for efficient swimming. Any circumstances which change this morphology can be expected to affect swimming efficiency and transport costs. Body size and shape in spotted dolphins varies with gender, geographic location, age, and reproductive status. In general, males are bigger than females, and both sexes are bigger closer to shore. Theoretically, larger individuals should be able to more easily evade tuna sets, although this possibility remains to be investigated. Reduced body size and swimming efficiency in young dolphins, and body shape changes during late pregnancy (when the midsection of female dolphins tends to become significantly more bulky and the flexibility of the tail stock more limited) can be expected to significantly increase hydrodynamic costs for both group. The question is potentially significant due to the sustained high number of

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dolphin sets continually occurring in the ETP, implying that numbers of affected young and late term pregnant female spotted dolphins also remains high. The incidence of chase during these life stages remains to be investigated.

Reproductive System. The calving interval (2-3 years) and lactation period (1-2 years) of spotted dolphins is shorter in the ETP than it is off the coast of Japan (4-6 years), perhaps reflecting the effects of prolonged exploitation on the life history parameters of ETP spotted dolphins. Alternatively, high prenatal mortality may be yielding an underestimate of calving interval; this latter interpretation is currently under investigation.

SUMMARY

In general, form and function of spotted dolphins appear typical of similarly-sized odontocetes, but some characteristics may predispose the species to negative effects from chase and capture by tuna purse-seiners in the ETP; these characteristics should be investigated further. Future research could be productively focused on (1) the acoustic environment created by tuna purse-seine set activities, with respect to potential for significant interference by fishery noise with spotted dolphin communications before, during, and after sets. Fishery-induced acoustic interference can be expected to interfere with mother-calf associations in particular, as well as with other inter-animal communications, and thus may affect survival, reproduction, and behavior, and (2) morphological and physical characteristics that appear likely to predispose particular life stages to more deleterious effects of fishery interactions, including sprinter vs. marathon muscle physiology, digestive system mobility, and age- and gender-related changes in cardiovascular and muscle systems, stress-resistence, and body size and shape. Investigating these questions could significantly improve our understanding of factors contributing to the apparently delayed recovery of spotted dolphins stocks in the ETP. Such future research should take into consideration the publication date of many of the studies reviewed here (often several decades past), to evaluate whether significant changes in environmental conditions, both natural and anthropogenic (e.g., diseases, contaminants, and new environmental stressors) may also need to be addressed.

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